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NEW YORK

FLORAL INVENTORY FOR THE U.S. ARMY PINON CANYON MANEUVER SITE, COLORADO

R.B. Shaw¹, S.L. Anderson¹, K.A. Schultz¹ & V.E. Diersing²

Department of Range Science, Colorado State University, Fort Collins,
Colorado 80523 USA

² Environmental Resources Team, Environmental Division, U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, Champaign, Illinois 61820 USA

ABSTRACT

The first objective in the U.S. Army's Land Condition/Trend Analysis Program is to complete a floristic inventory of their training lands. Plant specimens were collected from May 1985 through August 1988 at the Piñon Canyon Maneuver Site in southeastern Colorado. A total of 359 species of flowering plants were collected at the site. One taxon, Haplopappus fremontii Gray var. monocephalus (A. Nels.) Hall (Asteraceae), is proposed for the Federal Threatened and Endangered Species List. Three species [Portulaca parvula Gray, Sapindus saponaria L. var. drummondii (Hook. & Arn.) L. Benson and Amorpha nana Nutt.] are on the Colorado Natural Area List of Special Concern.

KEY WORDS: Floristics, Colorado, endangered species.

INTRODUCTION

One of the initial steps in implementing the U.S. Army's Land Condition/Trend Analysis Program (LCTA) is to do a complete floristic and vegetational inventory of military installations. In the spring of 1985 a study was begun at the Piñon Canyon Maneuver Site (PCMS) to describe the vegetation, produce a species and ecological checklist, and establish permanent field plots to determine the influence of tracked vehicular traffic on the native vegetation. The following species list is based on collections made from May 1985 through August 1988. Thus far, we have collected 359 species from 65 families and 220 genera. Voucher specimens for these collections are in the Range Science Herbarium, Colorado State University.

The 244,000 acre PCMS is located in southeastern Colorado (Figure 1). Average elevation at the site is approximately 5000 ft above sea level. The

region receives about 12 inches of precipitation each year. The climate is semiarid and temperate continental where maximum precipitation coincides with maximum temperature.

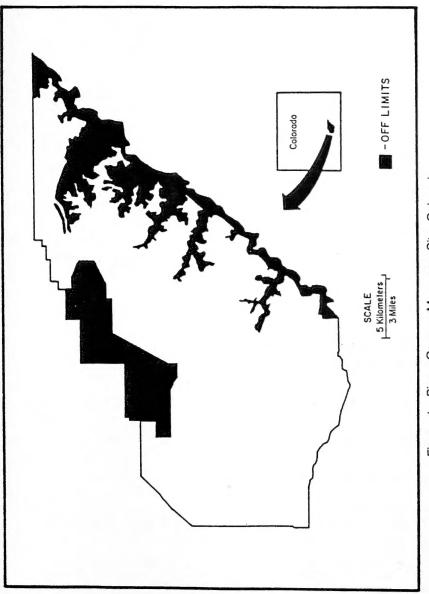
The vegetation at PCMS is a complex mosaic of grasslands, shrublands and woodlands. The mosaic of vegetation is due in part to the diverse soils (31 soil series or complexes reported) that have developed from sandstone, limestone, basalt and shale parent material. The dominant vegetation types are grasslands that cover extensive areas. These grasslands are typical of the shortgrass steppe or desert grassland and are dominated by blue grama (Bouteloua gracilis), black grama (B. eriopoda), western wheatgrass (Agropyron smithii) and galleta (Hilaria jamesii). Most common interstitial species are ring muhly (Muhlenbergia torreyi), tumblegrass (Schedonnardus paniculatus), squirreltail (Sitanion hystrix) and Fendler threeawn (Aristida fendleriana).

The shrublands at PCMS are, for the most part, composed of typical grassland understory vegetation with an overstory of shrubs or succulents. The most abundant erect succulent is tree cholla (Opuntia imbricata). Some of the most common shrubs are small soapweed (Yucca glauca, pale wolfberry (Lycium pallidum), common winterfat (Ceratoides lanata) and Bigelow sagebrush (Artemisia bigelovii). When soils are extremely sandy, sand sagebrush (A. filifolia) dominates the community. Alkali soils are typically dominated by dense stands of fourwing saltbush (Atriplex canescens) with an understory of alkali sacaton (Sporobolus airoides). Black greasewood (Sarcobatus vermiculatus) frequently is found in dense stands along seasonal streams and arroyos.

The woodlands are composed almost entirely of one seeded juniper (Juniperus monosperma) and pinyon pine (Pinus edulis). Understory shrubby vegetation tends to vary with parent material. On limestone outcrops, grease-bush (Glossopetalon meionandra), Bigelow sagebrush and James frankenia (Frankenia jamesii) are the most common shrubs. On sandstone parent material, the most common understory shrubs are wax currant (Ribes cereum), skunkbush sumac (Rhus trilobata), true mountain mahogany (Cercocarpus montanus), common hoptree (Ptelea trifoliata) and litteleaf mockorange (Philadelphus microphyllus). Riparian woodlands are dominated by plains cottonwood (Populus deltoides), willow (Salix sp.) and five-stamen tamarix (Tamarix pentandra).

The species list is in alphabetical order by family and species. Author citation, common synonyms, common name and a four letter symbol composed of the first two letters of the genus and specific epithet are given for each taxon. The first column after the common name refers to functional group (F=forb, G=grass, T=tree, S=shrub, \$=succulent and V=vine) The second column refers to whether the plant is native (N) or introduced (I). The





third column refers to the longevity of the plant (A=annual, B=biennial and P=perennial). The fourth column depicts whether the plant flowers during the cool season (C=March to June), warm season (W=July to September) or evergreen (E).

PLANT SPECIES LIST PIÑON CANYON MANEUVER SITE

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		Cool/Warm ity Season
AGAVACEAE				
Yucca glauca Nutt. SMALL SOAPWEED (YUGL)	S	N	P	C
ALISMATACEAE				
Alisma triviale Pursh (syn. A. plantago- aquatica L. var. americanum R. & S. AMERICAN WATERPLANTAIN (ALTR) F	N	P	w
cf <i>Alisma</i> sp. WATERPLANTAIN (AL-X)	F	N	P	C
Sagittaria cf latifolia Willd. COMMON ARROWHEAD (SALA)	F	N	P	w
AMARANTHACEAE				
Amaranthus albus L. TUMBLEWEED (AMAL1)	F	N	A	w
Amaranthus graecizans L. (syn. A. blitoides S. Wats.) PROSTRATE PIGWEED				
AMARANTH (AMGR)	F	N	Α	w

Alphabetic by Family Then by Species	Life Form In	Native/ ntroduced	Co Longevity	ool/Warm Season
AMARANTHACEAE (continued)				
Amaranthus retroflexus L. ROUGH PIGWEED (AMRE)	F	N	A	W
ANACARDIACEAE				
Rhus trilobata Nutt. SKUNKBUSH SUMAC (RHTR)	S	N	P	C
Toxicodendron rydbergii (Small) Greene POISON IVY (TORY)	V	N	P	С
APOCYNACEAE				
Apocynum cannabinum L. INDIAN HEMP (APCA)	F	N	P	С
ASCLEPIADACEAE				
Asclepias arenaria Torr. SAND MILKWEED (ASAR)	F	N	P	W
Asclepias asperula (Done.) Woodson (syncapricorn Woodson ssp. occidentalis Wo				
ANTELOPE HORNS (ASAS)	F	N	P	C
Asclepias engelmanniana Woodson ENGELMANN MILKWEED (ASEN)	F	I	P	W
Asclepias incarnata L. SWAMP MILKWEED (ASIN)	F	N	P	W
Asclepias macrotis Torr. LONGHORN MILKWEED (ASMA)	F	N	P	W
Asclepias speciosa Torr. SHOWY MILKWEED (ASSP)	F	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced	Co Longevity	ool/Warm Season
ASCLEPIADACEAE (continued)				
Asclepias subverticillata (Gray) Vail POISON MILKWEED (ASSU)	F	N	P	w
Asclepias verticillata L. WHORLED MILKWEED (ASVE)	F	N	P	w
WHORLED MILKWEED (ASVE)	Г	14	Р	VV
Asclepias viridiflora Raf. GREEN MILKWEED (ASVI)	F	N	P	w
BORAGINACEAE				
Cryptantha cinerea (Greene) Cronq. var.				
jamesii Cronq. [syn. C. jamesii (Torr.) F JAMES CRYPTANTHA (CRCI)	Pays.] F	N	P	C
Cryptantha minima Rydb.	_			
CRYPTANTHA (CRMI)	F	N	P	C
Cryptantha thyrsiflora (Greene) Payson CLUSTER CRYPTANTHA (CRTH)	F	N	Р.	C
Lappula diploma (F. & M.) Guerke [syn. L. redowskii (Hornem.) Greene var. cupulata (Gray) M.E. Jones; L. texana (Scheele) Britt.]				
CUPSEED STICKSEED (LADI)	F	N	Α	C
Lappula redowskii (Hornem.) Greene BLUEBUR STICKSEED (LARE)	F	N	A	C
Lithospermum incisum Lehm. NARROWLEAF GROMWELL (LIIN)	F	N	P	C
Onosmodium molle Michx. var.				
occidentale (Mack.) I. Johnst. WESTERN MARBLESEED (ONMO)	F	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
CACTACEAE				
Coryphantha vivipara (Nutt.) Britt. & Ros PINCUSHION CACTUS (COVI)	e \$	N	P	C
Echinocereus viridiflorus Engelm. HEDGEHOG CACTUS (ECVI)	\$	N	p	C
Opuntia imbricata (Haw.) DC. TREE CHOLLA (OPIM)	\$	N	P	C
Opuntia phaeacantha Engelm. PRICKLY PEAR (OPPH)	\$	N	P	C
Opuntia polyacantha Haw. var. polyacantha PLAINS PRICKLY PEAR (OPPO1)	\$	N	P	С
Opuntia polyacantha Haw. var. trichophora (Engelm. & Bigel.) Coult. HOARY PRICKLY PEAR (OPPO2)	\$	N	P	С
CAMPANULACEAE				
Lobelia cardinalis L. CARDINAL FLOWER (LOCA)	F	N	P	w
CAPPARIDACEAE				
Cleome serrulata Pursh ROCKY MOUNTAIN BEEPLANT (CLSE)	F	N	A	W
Polansia dodecandra (L.) DC. ssp. trachysperma (T. & G.) Iltis (syn. P. trachysperma T. & G.)				
CLAMMYWEED (PODO)	F	N	A	\mathbf{C}

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
CAPRIFOLIACEAE				
Sambucus canadensis L. AMERICAN ELDER (SACA)	S	N	P	w
Symphoricarpos occidentalis Hook. WESTERN SNOWBERRY (SYOC)	S	N	P	С
Symphoricarpos oreophilus Gray (syn. S. rotundifolius var. oreophilus M.E. Jones MOUNTAIN SNOWBERRY (SYOC)	s S	N	P	C
CARYOPHYLLACEAE				
Arenaria hookeri Nutt. var. hookeri HOOKER SANDWORT (ARHO)	F	N	P	С
Paronychia cf sessiliflora Nutt. CREEPING NAILWORT (PASE)	F	N	P	C
CELASTRACEAE				
Glossopetalon meionandra Koehne. [syn. Forsellesia meionandra (Koehne) Heller] GREASEBUSH (GLME)	S	N	p .	C
CHENOPODIACEAE				
Atriplex argentea Nutt. TUMBLING SALTBUSH (ATAR)	F	N	A	w
Atriplex canescens (Pursh) Nutt. FOURWING SALTBUSH (ATCA)	S	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
CHENOPODIACEAE (continued)				
Ceratoides lanata (Pursh) Howell				
[syn. Eurotia lanata (Pursh) Moq.] COMMON WINTERFAT (CELA)	S	N	P	C
Chenopodium cf album L.				
LAMBSQUARTERS GOOSEFOOT (CHAL)	F	I	A	W
Chenopodium incanum (S. Wats.) Heller GOOSEFOOT (CHIN)	F	N	A	W
Chenopodium cf leptophyllum Nutt. SLIMLEAF GOOSEFOOT (CHLE)	F	N	A	W
Kochia scoparia (L.) Schrad. KOCHIA (KOSC)	F	I	A	W
Salsola iberica Sennen & Pau				
(syn. <i>S. kali</i> L.) RUSSIAN THISTLE (SAIB)	F	I	A	W
Sarcobatus vermiculatus (Hook.) Torr. BLACK GREASEWOOD (SAVE)	S	N	P	С
COMMELINACEAE				
Tradescantia occidentalis (Britt.) B. Smyt. PRAIRIE SPIDERWORT (TROC)	h F	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced	Co Longevity	ool/Warm Season
COMPOSITAE				
Ambrosia cf acanthicarpa Hook. [syn. Franseria acanthicarpa (Hook.) Cov.] ANNUAL BURSAGE (AMAC)	F	N	A	w
Ambrosia psilostachya DC. var. coronopifolia (T. & G.) Farw. (syn. A. coronopifolia T. & G.	n	N	D	117
WESTERN RAGWEED (AMPS)	F	N	P	W
Antennaria obovata E. Nels. PUSSYTOES (ANOB)	F	N	P	C
Antennaria parvifolia Nutt. LITTLELEAF PUSSYTOES (ANPA)	F	N	P	C
Arctium minus Bernh. COMMON BURDOCK (ARMI)	F	I	В	w
Artemisia bigelovii Gray BIGELOW SAGEBRUSH (ARBI)	S	N	Ρ.	w
Artemisia dracunculus L. WILD TARRAGON (ARDR)	F	N	P	w
Artemisia filifolia Torr. SAND SAGEBRUSH (ARFI)	S	N	P	W
Artemisia frigida Willd. FRINGED SAGEBRUSH (ARFR)	F	N	P	W
Artemisia ludoviciana Nutt. LOUISIANA SAGEBRUSH (ARLU)	F	N	P	w
Aster of ericoides L. WHITE ASTER (ASER)	F	N	P	w

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
COMPOSITAE (continued)				
Aster cf falcatus Lindl. WHITEPRAIRIE ASTER (ASFA)	F	N	P	W
Baccharis wrightii Gray WRIGHT BACCHARIS (BAWR)	F	N	P	W
Brickellia cf brachyphylla (Gray) Gray BRICKELLBUSH (BRBR)	F	N	P	W
Brickellia cf californica (T. & G.) Gray CALIFORNIA BRICKELLBUSH (BRCA)	F	N	P	W
Centaurea repens L. (syn. C. picris Pall.) KNAPWEED (CERE1)	F	I	Р	W
Chrysothamnus nauseosus (Pall.) Britt. RABBITBRUSH (CHNA)	S	N	P	W
Cirsium cf undulatum (Nutt.) Spreng. WAVYLEAF THISTLE (CIUN)	F	N	В	W
Conyza canadensis (L.) Cronq. CANADIAN HORSEWEED (COCA)	F	I	A	W
Coreopsis tinctoria Nutt. PLAINS COREOPSIS (COTI)	F	I	A	W
Dyssodia aurca (Gray) A. Nels. DOGWEED (DYAU)	F	N	A	W
Erigeron divergens T. & G. var. cinereus Gray SPREADING FLEABANE (ERDI)	F	N	В	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
COMPOSITAE (continued)				
Erigeron pumilus Nutt. var. pumilus LOW FLEABANE (ERPU)	F	N	P	С
cf Evax prolifera Nutt. FLUFFWEED (EVPR)	F	N	Α	C
Gaillardia pinnatifida Torr. BLANKET FLOWER (GAPI)	F	N	P	C
Grindelia squarrosa (Pursh) Dun. CURLYCUP GUMWEED (GRSQ)	F	N	P	w
Gutierrezia sarothrae (Pursh) Britt. & Rusby [syn. Xanthocephalum sarothrae (Pursh) Shinners] BROOM SNAKEWEED (GUSA)	F	N	P	w
Haplopappus fremontii Gray var. fremonti [syn. Oonopsis foliosa (Gray) Greene] FREMONT GOLDENWEED (HAFR1)	i F	N	P	w
Haplopappus fremontii Gray var. monocephalus (Nels.) Hall (syn. Oonopsis monocephala A. Nels. RAYLESS GOLDENWEED (HAFR2)	F	N	Р	w
Haplopappus spinulosus (Pursh) DC. [syn. Machaeranthera pinnatifida (Hook.) Shinners]				
SPINY GOLDENWEED (HASP) Helianthus petiolaris Nutt.	F	N	P	С
PRAIRIE SUNFLOWER (HEPE)	F	N	A	W
Helianthus sp. SUNFLOWER (HE-X)	F		A	W

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
COMPOSITAE (continued)				
Heterotheca horrida (Rydb.) V. Harms [syn. Chrysopsis hispida (Hook.) DC.; Chrysopsis horrida Rydb.] GOLDASTER (HEHO)	F	N	P	W
Heterotheca villosa (Pursh) Shinners var. angustifolia (Rydb.) V. Harms [syn. Chrysopsis villosa (Pursh) Nutt.; var. angustifolia (Rydb.) Cronq.] HAIRY GOLDASTER (HEVI)	F	N	P	W
Hymenopappus filifolius Hook. FINE LEAF HYMENOPAPPUS (HYFI)	F	N	P	С
Hymenopappus tenuifolius Pursh HYMENOPAPPUS (HYTE)	F	N	В	С
Hymenoxys acaulis (Pursh) Parker STEMLESS HYMENOXYS (HYAC)	F	N	P	С
Iva axillaris Pursh POVERTYWEED (IVAX)	F	N	P	W
Lactuca serriola L. (syn. L. scariola L.) PRICKLY LETTUCE (LASE)	F	I	A	W
Lactuca tatarica (L.) C.A. Meyer ssp. pulchella (Pursh) Stebbins [syn. L. pulche (Pursh) Stebbins; L. oblongifolia Nutt.] CHICORY LETTUCE (LATA)	ella F	N	P	w
Leucelene ericoides (Torr.) Greene [syn. Aster arenosus (Heller) Blake] HEATH ASTER (LEER)	F	N	P	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
COMPOSITAE (continued)				
Liatris punctata Hook. DOTTED GAYFEATHER (LIPU)	F	N	P .	w
<i>Lygodesmia juncea</i> (Pursh) Hook. RUSH SKELETONPLANT (LYJU)	F	N	P	w
Melampodium cinereum DC. [syn. M. leucanthum T. & G. PLAINS BLACKFOOT (MECI)	F	N	P	С
Nothocalais cuspidata (Pursh) Greene [syn. Microseris cuspidata (Pursh) Sch.] FALSE DANDELION (NOCU)	F	N	P	C
Palafoxia rosea (Bush) Cory var. macrolep Rydb. [syn. P. macrolepis (Rydb.) Cory] PALAFOXIA (PARO)		N	A	w
Pectis angustifolia Torr. FETID-MARIGOLD (PEAN1)	F	N	A	w
Picradeniopsis oppositifolia (Nutt.) Rydb. [syn. Bahia oppositifolia (Nutt.) DC.] PLAINS BAHIA (PIOP)	F	N	P	W
Ratibida columnifera (Nutt.) Wooton & Standley UPRIGHT PRAIRIE CONEFLOWER (RACO)	F	N	P	w
Ratibida tagetes (James) Barnh. SHORTRAY PRAIRIE CONEFLOWER (RATA)	F	N	P	W

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
COMPOSITAE (continued)				
Senecio cf pseudaureus Rydb. var. flavulus (Greene) Greenm. (syn. S. flavulus Green GOLDEN GROUNDSEL (SEPS)	e) F	N	P	С
Senecio riddellii T. & G. RIDDELL GROUNDSEL (SERI)	F	N	P	W
Senecio tridenticulatus Rydb. GROUNDSEL (SETR)	F	N	P	C
Solidago mollis Bartl. VELVETY GOLDENROD (SOMO)	F	N	P	W
Solidago multiradiata Ait. (syn. S. ciliosa Greene) GOLDENROD (SOMU)	F	N	P	W
Solidago petiolaris Ait. DOWNY GOLDENROD (SOPE)	F	N	P	W
Solidago sparsiflora Fray THREE-NERVED GOLDENROD (SOSI	P) F	N	P	W
Stephanomeria pauciflora (Torr.) A. Nels. DESERT WIRELETTUCE (STPA)	F	N	P	W
Taraxacum officinale Weber COMMON DANDELION (TAOF)	F	I	P	C
Thelesperma megapotamicum (Spreng.) O. GREENTHREAD (THME)	Ktze. F	N	P	С
Thelesperma subnudum Gray NAVAJO-TEA GREENTHREAD (THSU	U) F	N	Р	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
COMPOSITAE (continued)				
Townsendia hookeri Beaman EASTER DAISY (TOHO)	F	N	P	C
Tragopogon dubius Scop. WESTERN SALSIFY (TRDU)	F	I	В	C
Verbesina encelioides (Cav.) Benth. & Hoo GOLDEN CROWNBEARD (VEEN)	ok. F	N	Α	W
Xanthium strumarium L. COCKLEBUR (XAST)	F	I	Α	w
Zinnia grandiflora Nutt. ROCKY MOUNTAIN ZINNIA (ZIGR)	F	N	P	C
CONVOLVULACEAE				
Convolvulus arvensis L. ' FIELD BINDWEED (COAR)	V	I	P	C
Convolvulus equitans Benth. BINDWEED (COEQ)	V	N _.	P	w
Evolvulus nuttallianus R. & S. ARIZONA EVOLVULUS (EVNU)	F	N	P	С
Ipomoea leptophylla Torr. BUSH MORNING-GLORY (IPLE)	v	N	P	С
CRUCIFERAE				
Camelina microcarpa Andrz. LITTLEPOD FALSEFLAX (CAMI)	F	I	A	С
Descurainia pinnata (Walt.) Britt. PINNATE TANSYMUSTARD (DEPI)	F	N	A	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
CRUCIFERAE (continued)				
Descurainia sophia (L.) Webb. FLIXWEED TANSYMUSTARD (DESO)	F	I	Α	С
Draba reptans (Lam.) Fern. CAROLINA DRABA (DRRE)	F	N	A	C
Erysimum asperum (Nutt.) DC. WESTERN WALLFLOWER (ERAS)	F	N	P	C
Lesquerella fendleri (Gray) Wats. FENDLERS BLADDERPOD (LEFE)	F	N	P	C
Stanleya pinnata (Pursh) Britt. PRINCES PLUME (STPI)	F	N	P	C
Thelypodium wrightii Gray WRIGHT THELYPODY (THWR)	F	N	В	w
CUCURBITACEAE				
Cucurbita foetidissima H.B.K. BUFFALO GOURD (CUFO)	V	I	P	W
CUPRESSACEAE				
Juniperus monosperma (Engelm.) Sarg. ONESEEDED JUNIPER (JUMO)	Т	N	P	С
Juniperus scopulorum Sarg. ROCKY MOUNTAIN JUNIPER (JUSC)) Т	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced	Co Longevity	ool/Warm Season
CYPERACEAE				
Carex brevoir (Dew.) Mack. SEDGE (CABR)	F	N	P	C
Carex foena Willd. SEDGE (CAFO)	F	N	P	C
Carex gravida Bailey var. lunelliana (Mack.) F.J. Herm. HEAVY SEDGE (CAGR)	F	N	P	C
Carex cf lanuginosa Michx. WOOLLY SEDGE (CALA)	F	N	P	С
Carex xerantica Bailey SEDGE (CAXE)	F	N	P	C
Cyperus filiculmis Vahl. [syn. C. lupulinus (Spreng.) Marcks ssp. lupulinus] FERN FLATSEDGE (CYFI)	F	N	P	w
Cyperus schweinitzii Torr. SCHWEINITZ FLATSEDGE (CYSC)	F	N	P ·	w
Eleocharis palustris (L.) R. & S. (syn. E. macrostachya Britt.) COMMON SPIKESEDGE (ELPA)	F	N	P	C
Eleocharis sp. SPIKESEDGE (EL-X)	F		P	C
Scirpus acutus Muhl. TULE BULRUSH (SCAC)	F	N	P	С
Scirpus americanus Pers. AMERICAN BULRUSH (SCAM)	F	N	P	W
Scirpus pallidus (Britt.) Fern. BULRUSH (SCPA1)	F	N	P	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
EQUISETACEAE				
Equisetum laevigatum A. Braun SMOOTH HORSETAIL (EQLA)	F	N	Р	С
$Equisetum\ variegatum\ Schleich.$ VARIEGATED HORSETAIL (EQVA)	F	N	P	W
EUPHORBIACEAE				
Croton texensis (Kl.) Muell. Arg. TEXAS CROTON (CRTE)	F	N	Α	W
Euphorbia dentata Michx. TOOTHED EUPHORBIA (EUDE)	F	N	Α	C
Euphorbia fendleri T. & G. FENDLER EUPHORBIA (EUFE)	F	N	P	C
Euphorbia cf glyptosperma Engelm. RIDGESEED EUPHORBIA (EUGL)	F	N	A	С
Euphorbia lata Engelm. HOARY EUPHORBIA (EULA)	F	N	P	C
Euphorbia marginata Pursh SNOW-ON-THE-MOUNTAIN- EUPHORBIA (EUMA)	F	N	A	W
Euphorbia missurica Raf. [syn. Chamaesyce missurica (Raf.) Shinners] MISSOURI EUPHORBIA (EUMI)	F	N	A	W
Euphorbia cf serpens H.B.K. ROUND LEAVED SPURGE (EUSE)	F	N	A	W
Euphorbia spathulata Lam. SPURGE (EUSP)	F	N	A	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
EUPHORBIACEAE (continued)				
Euphorbia stictospora Engelm. MAT SPURGE (EUST)	F	N	A	W
Tragia nepetaefolia Cav. (syn. T. urticifoli Michx.; T. betonicifolia Nutt. NOSEBURN (TRNE)	a F	N	P	С
FRANKENIACEAE				
Frankenia jamesii Torr. JAMES FRANKENIA (FRJA)	S	N	P	С
FUMARIACEAE				
Corydalis aurea Willd. GOLDEN SMOKE (COAU)	F	N	A	C
GERANIACEAE				
Erodium cicutarium (L.) L'Her. FILAREE (ERCI1)	F	I	A	C
GRAMINEAE				
Agropyron cristatum (L.) Gaertn. CRESTED WHEATGRASS (AGCR)	G	I	P	C
Agropyron dasystachyum (Hook.) Scribn. THICKSPIKE WHEATGRASS (AGDA)	G	N	P	C
Agropyron smithii Rydb. WESTERN WHEATGRASS (AGSM)	G	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
GRAMINEAE (continued)				
Agrostis stolonifera L. REDTOP BENTGRASS (AGST)	G	I	P	C
Andropogon gerardii Vitman BIG BLUESTEM (ANGE)	G	N	P	W
Aristida adscensionis L. SIXWEEKS THREEAWN (ARAD)	G	N	Α	W
Aristida divaricata Humb. & Bonpl. POVERTY THREEAWN (ARDI)	G	N	P	W
Aristida fendleriana Steud. [syn. A. purpu Nutt. var. longiseta (Steud.) Vasey] FENDLER THREEAWN (ARFE)	irea G	N	P	W
Aristida longiseta Steud. [syn. A. purpure Nutt. var. robusta (Merrill) A. Holmgren & N. Holmgren] RED THREEAWN (ARLO)	a G	N	P	W
Aristida purpurea Nutt. PURPLE THREEAWN (ARPU)	G	N	P	W
Avena fatua L. WILD OAT (AVFA)	G	I	A	С
Bothriochloa saccharoides (Sw.) Rydb. (syn. Andropogon saccharoides Sw.) SILVER BLUESTEM (BOSA)	G	N	P	W
Bouteloua curtipendula (Michx.) Torr. SIDEOATS GRAMA (BOCU)	G	N	P	W
Bouteloua eriopoda (Torr.) Torr. BLACK GRAMA (BOER)	G	N	P	W

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
GRAMINEAE (continued)				
Bouteloua gracilis (H.B.K.) Lag. BLUE GRAMA (BOGR)	G	N	P	w
Bouteloua hirsuta Lag. HAIRY GRAMA (BOHI)	G	N	P	w
Bromus japonicus Thunb. JAPANESE BROME (BRJA)	G	I	A	C
Buchloe dactyloides (Nutt.) Engelm. BUFFALOGRASS (BUDA)	G	N	P	W
Calamagrostis neglecta (Ehrh.) Gaertn. [syn. C. stricta (Timm.) Koel.] SLIMSTEM REEDGRASS (CANE)	G	N	P	C
Cenchrus longispinus (Hack.) Fern. SANDBUR (CELO)	G	N	P	W
Dactylis glomerata L. ORCHARDGRASS (DAGL)	G	I	Р.	С
Dichanthelium oligosanthes (Schult.) Gould var. scribnerianum (Nash) Gould (syn. Panicum scribnerianum Nash) SCRIBNER PANICUM (DIOL)	G	N	P	C
Distichlis spicata (L.) Greene var. stricta (Torr.) Beetle INLAND SALTGRASS (DISP)	G	N	P	w
Echinochloa crusgalli (L.) Beauv. BARNYARD GRASS (ECCR)	G	I	A	w

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
GRAMINEAE (continued)				
Elymus canadensis L. CANADA WILDRYE (ELCA)	G	N	P	С
Eragrostis cilianensis (All.) Mosher STINK GRASS (ERCI2)	G	N	A	W
Eragrostis spectabilis (Pursh) Steud. PURPLE LOVEGRASS (ERSP)	G	N	P	W
Erioneuron pilosum (Buckl.) Nash [syn. Tridens pilosus (Buckl.) Hitchc.] HAIRY FALSE TRIDENS (ERPI)	G	N	P	W
Glyceria stricta (Lam.) Hitchc. FOWL MANNAGRASS (GLST)	G	N	P	C
Hilaria jamesii (Torr.) Benth. GALLETA (HIJA)	G	N	P	W
Hordeum jubatum L. FOXTAIL BARLEY (HOJU)	G	N	P	С
Hordeum pusillum Nutt. LITTLE BARLEY (HOPU)	G	N	A	С
Koeleria pyramidata (Lam.) Beauv. [syn. K. cristata (L.) Pers.] PRAIRIE JUNEGRASS (KOPY)	G	N	P	C
Lycurus phleoides H.B.K. COMMON WOLFTAIL (LYPH)	· G	N	P	W
Muhlenbergia arenacea (Buckl.) Hitchc. EAR MUHLY (MUAR1)	G	N	P	W

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
GRAMINEAE (continued)				
Muhlenbergia arenicola Buckl. SAND MUHLY (MUAR2)	G	N	P	W
Muhlenbergia asperifolia (Nees. & Mey.) Parodi				
ALKALI MUHLY (MUAS)	G	N	P	W
Muhlenbergia racemosa (Michx.) B.S.P. GREEN MUHLY (MURA)	G	N	P	w
Muhlenbergia torreyi (Kunth) Hitchc. RING MUHLY (MUTO)	G	N	P	w
Munroa squarrosa (Nutt.) Torr. FALSE BUFFALOGRASS (MUSQ)	G	N	A	w
Oryzopsis hymenoides (R. & S.) Ricker INDIAN RICEGRASS (ORHY)	G	N	P	C
Oryzopsis micrantha (Trin. & Rupr.) Thu LITTLESEED RICEGRASS (ORMI)	rb. G	N	Р.	C
Panicum capillare L. COMMON WITCHGRASS (PACA)	G	N	A	w
Panicum obtusum H.B.K. VINE MESQUITE (PAOB)	G	N	P	w
Panicum virgatum L. SWITCHGRASS (PAVI2)	G	N	P	w
Phleum pratense L. TIMOTHY (PHPR)	G	I	P	С
Phragmites communis Trin. [syn. P. australis (Cav.) Trin.] COMMON RED REED (PHCO)	G	N	P	С

Alphabetic by Family Then by Species	Life	Native/ Introduced		ool/Warm
Their by Species			Dongevity	
GRAMINEAE (continued)				
Poa bigelovii Vasey & Scribn. BIGELOW BLUEGRASS (POBI)	G	N	P	С
Poa pratensis L. KENTUCKY BLUEGRASS (POPR)	G	I	P	С
Poa sandbergii Vasey SANDBERG BLUEGRASS (POSA)	G	N	P	С
Polypogon monspeliensis (L.) Desf. RABBITFOOT POLYPOGON (POMO)	G	I	Α	С
Schedonnardus paniculatus (Nutt.) Trel. TUMBLEGRASS (SCPA2)	G	N	P	W
Schizachyrium scoparium (Michx.) Nash (syn. Andropogon scoparius Michx.) LITTLE BLUESTEM (SCSC)	G	N	Р	W
Scleropogon brevifolius Phil. BURROGRASS (SCBR)	G	Ν	P	W
Sitanion hystrix Nutt. J.G. Smith SQUIRRELTAIL (SIHY)	G	N	P	С
Sorghastrum nutans (L.) Nash INDIANGRASS (SONU2)	G	N	Р	W
Sphenopholis obtusata (Michx.) Scribn. WEDGEGRASS (SPOB)	G	N	Р	С
Sporobolus airoides (Torr.) Torr. ALKALI SACATON (SPAI)	G	N	P	W

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
GRAMINEAE (continued) Sporobolus cryptandrus (Torr.) Gray SAND DROPSEED (SPCR)	G	N	P	w
Stipa comata Trin. & Rupr. NEEDLE AND THREAD (STCO)	G	N	P	C
Stipa neomexicana (Thurb.) Scribn. NEW MEXICO FEATHERGRASS (STNE)	G	N	P	C
Stipa robusta (Vasey) Scribn. SLEEPYGRASS (STRO)	G	N	P	C
Stipa scribneri Vasey SCRIBNER NEEDLEGRASS (STSC)	G	N	P	С
Stipa viridula Trin. GREEN NEEDLEGRASS (STVI)	G	N	P	C
Tridens elongatus (Buckl.) Nash [syn. T. muticus (Torr.) Nash var. elongatus (Buckl. Shinners] GREEN TRIDENS (TREL)	G	N	р .	w
Vulpia octoflora (Walt.) Rydb. (syn. Festuca octoflora Walt.) SIXWEEKS FESCUE (VUOC)	G	N	A	C
GROSSULARIACEAE				
Ribes aureum Pursh GOLDEN CURRANT (RIAU)	S	N	P	C
Ribes cereum Dougl. WAX CURRANT (RICE)	S	N	P	C
Ribes of leptanthum Gray TRUMPET GOOSEBERRY (RILE)	S	N	p	C

Alphabetic by Family		Native/		ool/Warm	
Then by Species	Form	Introduced	Longevity	Season	
HYDRANGEACEAE					
Philadelphus microphyllus Gray var. microphyllus LITTLELEAF MOCKORANGE (PHMI)	S	N	p	С	
JUNCACEAE					
Juncus balticus Willd. BALTIC RUSH (JUBA)	F	N	P	С	
Juncus interior Wieg. INLAND RUSH (JUIN)	F	N	P	С	
Juncus torreyi Cov. TORREY RUSH (JUTO)	F	N	P	W	
LABIATAE					
Hedeoma drummondii Benth. DRUMMOND FALSE PENNYROYAL (HEDR)	F	N	P	С	
Marrubium vulgare L. COMMON HOARHOUND (MAVU)	F	I	P	С	
Monarda pectinata Nutt. PONY BEEBALM (MOPE)	F	N	A	С	
Salvia reflexa Hornem. LANCELEAF SAGE (SARE)	F	N	A	W	
Teucrium laciniatum Torr. CUTLEAF GERMANDER (TELA)	F	N	P	С	

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
LEGUMINOSAE				
Amorpha fruticosa L. FALSE INDIGO (AMFR)	S	N	P	C
Amorpha nana Nutt.				
DWARF INDIGO AMORPHA (AMNA)	S	N	P	C
Astragalus crassicarpus Nutt. GROUNDPLUM MILKVETCH (ASCR)	F	N	P	C
Astragalus gracilis Nutt.	•		•	
SLENDER MILKVETCH (ASGR)	F	N	P	C
Astragalus missouriensis Nutt. MISSOURI MILKVETCH (ASMI)	F	N	P	C
Astragalus puniceus Osterh. TRINIDAD MILKVETCH (ASPU)	F	N	P	C
Astragalus racemosus Pursh ALKALI MILKVETCH (ASRA)	F	N	P	C
Astragalus shortianus Nutt. SHORTS MILKVETCH (ASSH)	F	N	P	C
Caesalpinia jamesii (T. & G.) Fisher (syn. Hoffmanseggia jamesii T. & G. JAMES RUSHPEA (CAJA)	F	N	P	C
Dalea aurea Nutt. SILKTOP DALEA (DAAU)	F	N	P	w

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
LEGUMINOSAE (continued)				
Dalea candida Michx. [syn. Petalostemum candidus (Willd.) Michx. WHITE PRAIRIE CLOVER (DACA)	F	N	P	C
Dalea enneandra Nutt. INDIGO BUSH (DAEN)	F	N	P	W
Dalea jamesii (Torr.) T. & G. JAMES DALEA (DAJA)	F	N	P	С
Dalea purpurea Vent. [syn. Petalostemum purpureum (Vent.) Rydb. PURPLE PRAIRIE CLOVER (DAPU)	F	N	P	C
Glycyrrhiza lepidota Pursh AMERICAN LICORICE (GLLE)	F	N	P	С
Hedysarum boreale Nutt. NORTHERN SWEETVETCH (HEBO)	F	N	P	W
Hoffmanseggia drepanocarpa Gray SICKLEPOD RUSHPEA (HODR)	F	N	P	С
Lathyrus eucosmus Butters & St. John [syn. L. brachycalyx Rydb. ssp. eucosmus (Butters & St. John) Welsh] BUSH PEAVINE (LAEU)	F	N	P	C
Lupinus pusillus Pursh RUSTY LUPINE (LUPU)	F	N	A	C
Melilotus alba Medic. WHITE SWEETCLOVER (MEAL1)	F	I	A	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
Melilotus officinalis (L.) Pallas YELLOW SWEETCLOVER (MEOF)	F	I	A	C
Oxytropis lambertii Pursh LAMBERT CRAZYWEED (OXLA)	F	N	P	C
Psoralea tenuiflora Pursh SLIMFLOWER SCURFPEA (PSTE)	F	N	P	C
Sophora nuttalliana B.L. Turner (syn. S. sericea Nutt.) SILKY SOPHORA (SONU1)	F	N	P	C
Vicia americana Muhl. AMERICAN VETCH (VIAM)	v	N	P	C
LILIACEAE				
Allium textile A. Nels. & Macbr. TEXTILE ONION (ALTE)	F	N	P	C
Calochortus cf gunnisonii S. Wats. GUNNISON MARIPOSALILY (CAGU)	F	N	Р.	C
Leucocrinum montanum Nutt. SAND LILY (LEMO) LINACEAE	F	N	P	С
Linum lewisii Pursh [syn. L. perenne L. var. lewisii (Pursh) Eat. & Wright] LEWIS FLAX (LILE)	F	N	P	C
Linum cf rigidum Pursh YELLOW FLAX (LIRI)	F	N	A	С

Alphabetic by Family	Life	Native/	Cool/Warm	
Then by Species	Form	Introduced	Longevity	Season
LOASACEAE				
Mentzelia albicaulis (Hook.) T. & G. WHITESTEM MENTZELIA (MEAL2)	F	N	A	С
Mentzelia nuda (Pursh) T. & G. [syn. Nuttallia nuda (Pursh) Greene] BRACTLESS MENTZELIA (MENU)	F	N	P	W
Mentzelia oligosperma Nutt. STICKLEAF (MEOL)	F	N	P	W
MALVACEAE				
Sphaeralcea angustifolia (Cav.) D. Don [syn. S. angustifolia (Cav.) D. Don var. cuspidata] NARROWLEAF GLOBEMALLOW				
(SPAN)	F	N	P	С
Sphaeralcea coccinea (Pursh) Rydb. SCARLET GLOBEMALLOW (SPCO)	F	N	P	С
MARTYNIACEAE				
Martynia louisianica P. Mill. [syn. Proboscidea louisianica (P. Mill.) Thell.] DEVIL'S CLAW (MALO)	F	N	A	W
NYCTAGINACEAE				
Abronia fragrans Nutt. SNOWBALL SANDVERBENA (ABFR)	F	N	P	С
Mirabilis multiflora (Torr.) Gray COLORADO FOUR-O'CLOCK (MIMU) F	N	P	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
NYCTAGINAÇEAE (continued)				
Mirabilis hirsuta (Pursh) MacM. (syn. Oxybaphus hirsutus Sweet) HAIRY UMBRELLAWORT (MIHI)	F	N	P	C
Mirabilis linearis (Pursh) Heimerl. [syn. Oxybaphus linearis (Pursh) Robinso NARROWLEAVED UMBRELLAWORT (MILI)		N	р	C
Tripterocalyx micranthus (Torr.) Hook. SANDPUFF (TRMI)	F	N	P	С
ONAGRACEAE				
Calylophus hartwegii (Benth.) Raven ssp. lavandulifolius (T. & G.) Towner & Rave [syn. C. lavandulifolius (T. & G.) Raven; Oenothera lavandulaefolia T. & G.] LAVENDERLEAF EVENING	n			
PRIMROSE (CAHA)	F	N	P	C
Gaura coccinea Pursh SCARLET GAURA (GACO)	F	N	P	C
Gaura parviflora Dougl. SMALLFLOWER GAURA (GAPA)	F	N	В	C
Oenothera caespitosa Nutt. TUFTED EVENING PRIMROSE (OECA)	F	N	P	C
Oenothera harringtonii Wagner, Stockhou & Klein EVENING PRIMROSE (OEHA)	se F	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
OROBANCHACEAE				
Orobanche multiflora Nutt. BROOMRAPE (ORMU)	F	N	P	W
PAPAVERACEAE				
Argemone cf hispida Gray [syn. A. platyceras Link. & Otto var. hispida (Gr. HEDGEHOG PRICKLYPOPPY (ARHI)	ay) Pra F	in] N	P	С
PINACEAE				
Pinus edulis Engelm. PINYON PINE (PIED)	Т	N	P	Е
Pinus ponderosa Dougl. PONDEROSA PINE (PIPO)	Т	N	P	E
PLANTAGINACEAE				
Plantago patagonica Jacq. (syn. P. purshii R. & S.) WOOLLY PLANTAIN (PLPA)	F	N	A	С
POLEMONIACEAE				
Gilia acerosa (Gray) Britt. (syn. G. rigidula Benth. GILIA (GIAC)	F	N	P	C
Ipomopsis laxiflora (Coult.) V. Grant (syn. Gilia laxiflora (Coult.) Osterh. GILIA (IPLA)	F	N	A	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced	Congevity	ool/Warm Season
POLEMONIACEAE (continued)				
Ipomopsis pumila (Nutt.) V. Grant				
(syn. Gilia pumila Nutt.)				
DWARF GILIA (IPPU)	F	N	Α	C
Ipomopsis spicata (Nutt.) V. Grant (syn. Gilia spicata Nutt.				
SPIKE GILIA (IPSP)	F	N	P	C
Phlox longifolia Nutt.				
LONGLEAF PHLOX (PHLO)	F	N	P	C
POLYGONACEAE				
Eriogonum annuum Nutt. ANNUAL ERIOGONUM (ERAN)	F	N	A	W
Eriogonum effusum Nutt.				
BUSHY ERIOGONUM (EREF)	F	N	P	W
Eriogonum jamesii Benth. var. jamesii JAMES ERIOGONUM (ERJA)	F	N	Р .	W
Eriogonum lachnogynum Torr.				
ERIOGONUM (ERLA)	F	N	P	W
Eriogonum tenellum Torr. MATTED WILD BUCKWHEAT				
(ERTE)	F	N	P	W
Eriogonum cf umbellatum Torr.	T)	NT.	n	111
SULPHUR ERIOGONUM (ERUM)	F	N	P	W

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
POLYGONACEAE (continued)				
Rumex crispus L. CURLY DOCK (RUCR)	F	I	P	С
Rumex stenophyllus Ledeb. NARROWLEAF DOCK (RUST)	F	I	P	С
POLYPODIACEAE				
Woodsia oregana D.C. Eaton OREGON WOODSIA (WOOR)	F	N	Р	C
PORTULACACEAE				
Portulaca oleracea L. COMMON PURSLANE (POOL)	F	N	Α	С
Portulaca parvula Gray PURSLANE (POPA)	F	N	A	С
Talinum parviflorum Nutt. PRAIRIE FAMEFLOWER (TAPA)	F	N	P	W
RANUNCULACEAE				
Clematis ligusticifolia Nutt. WESTERN VIRGINSBOWER (CLLI)	V	N	P	W.
Delphinium cf virescens Nutt. ssp. penardii (Huth) Ewan PLAINS LARKSPUR (DEVII)	F	N	P	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
RANUNCULACEAE (continued)				
Delphinium virescens Nutt. ssp. wootonii (Rydb.) Ewan (syn. D. wootonii Rydb.) WOOTON LARKSPUR (DEVI2)	F	N	P	C
ROSACEAE				
Amelanchier alnifolia Nutt. SASKATOON SERVICEBERRY (AMAL)	S	N	P	C
Cercocarpus montanus Raf. TRUE MOUNTAIN MAHOGANY (CEMO)	S	N	P	C
Physocarpus monogynus (Torr.) Coult. MOUNTAIN NINEBARK (PHMO)	S	N	P	C
Potentilla cf arguta Pursh var. arguta WHITE CINQUEFOIL (POAR)	F	N	Ρ.	w
Prunus americana Marsh. AMERICAN PLUM (PRAM)	S	N	P	C
Prunus pensylvanica L. f. PIN CHERRY (PRPE)	Т	N	P	C
Prunus virginiana L. COMMON CHOKECHERRY (PRVI)	S	N	P	C
Rosa cf woodsii Lindl. WOOD ROSE (ROWO)	S	N	P	С
Rubus deliciosus Torr. BOULDER RASPBERRY (RUDE)	S	N	P	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
RUTACEAE				
Ptelea trifoliata L. (syn. P. baldwinii T. & G.) COMMON HOPTREE (PTTR)	S	N	P	С
SALICACEAE				
Populus deltoides Marsh. ssp. monilifera (Ait.) Eckenw.; syn. P. sargentii Dode) PLAINS COTTONWOOD (PODE)	Т	N	P	C
Populus tremuloides Michx.	1	14	1	O
QUAKING ASPEN (POTR)	Т	N	P	C
Salix cf amygdaloides Anderss. PEACHLEAF WILLOW (SAAM)	Т	N	P	С
Salix exigua Nutt. ssp. interior (Rowlee) Cronq. (syn. S. interior Rowle SANDBAR WILLOW (SAEX)	e) S	N	P	C
Salix sp. WILLOW (SA-X)	S		Р	С
SANTALACEAE				
Comandra umbellata (L.) Nutt. BASTARD TOADFLAX (COUM)	F	N	Р	С
SAPINDACEAE				
Sapindus saponaria L. var. drummondii (Hook. & Arn.) L. Benson (syn. S. drummondii Hook. & Arn.) SOUTHERN SOAPBERRY (SASA)	Т	N	P	С

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
SAXIFRAGACEAE				
Heuchera parvifolia Nutt. LITTLELEAF ALUMROOT (HEPA)	F	N	P	C
SCROPHULARIACEAE				
Castilleja integra Gray ORANGE PAINTBRUSH (CAIN)	F	N	P	C
Castilleja sessiliflora Pursh DOWNY PAINTBRUSH (CASE)	F	N	P	C
Penstemon angustifolius Nutt. var. caudatus (Heller) Rydb. NARROWLEAF PENSTEMON (PEAN2)	F	N	P	C
Penstemon auriberbis Pennell PENSTEMON (PEAU)	F	N	P	С
Penstemon barbatus (Cav.) Roth. var. torreyi (Benth.) Keck TORREY PENSTEMON (PEBA) Verbascum thapsus L.	F	N	P	W
FLANNEL MULLEIN (VETH)	F	I	В	С
SOLANACEAE				
Chamaesaracha coronopus (Dun.) Gray GREEN FALSE NIGHTSHADE (CHCO)	F	N	P	C
Lycium pallidum Miers PALE WOLFBERRY (LYPA)	S	N	P	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
Physalis hederifolia Gray var. cordifolia (Gray) Waterfall (syn. Physalis fendleri Gray) CLAMMY GROUNDCHERRY (PHHE)	F	N	P	W
Physalis lobata Torr. [syn. Quincula lobata (Torr.) Raf.] PURPLEFLOWER GROUNDCHERRY (PHLO1)	F	N	P	С
Physalis longifolia Nutt. var. longifolia [syn. P. virginiana P. Mill. var. sonorae (Torr.) Waterfall LONGLEAF GROUNDCHERRY (PHLO2)	F	N	P	C
Physalis longifolia Nutt. var. subglabrata (Mack. & Bush) Cronq. (syn. P. subglabrata Mack & Bush) TAPERLEAF GROUNDCHERRY (PHLO3)	F	N	P	C
Solanum elaeagnifolium Cav. SILVERLEAF NIGHTSHADE (SOEL)	F	N	P	С
Solanum nigrum L. (syn. S. ptycanthum Dun.) BLACK NIGHTSHADE (SONI)	F	I	A	C
Solanum rostratum Dun. BUFFALOBUR NIGHTSHADE (SORO) F	N	A	W
Solanum triflorum Nutt. CUTLEAF NIGHTSHADE (SOTR)	F	N	A	C

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
TAMARICACEAE				
Tamarix pentandra Pallas (syn. T gallica L.) FIVE-STAMEN TAMARIX (TAPE)	S	I	P	C
TYPHACEAE				
Typha angustifolia L. NARROWLEAF CATTAIL (TYAN)	F	N	P	C
Typha latifolia L. COMMON CATTAIL (TYLA)	F	N	P	C
ULMACEAE				
Celtis reticulata Torr. NETLEAF HACKBERRY (CERE2)	Т	N	P	С
UMBELLIFERAE				
Conium maculatum L. POISON HEMLOCK (COMA)	F	I	В	C
Cymopterus montanus T. & G. MOUNTAIN SPRING PARSLEY (CYMO)	F	N	P	C
Lomatium orientale Coult. & Rose ORIENTAL LOMATIUM (LOOR)	F	N	P	C
Musineon divaricatum (Pursh) Nutt. LEAFY MUSINEON (MUDI)	F	N	P	C

Shaw et al.:

Alphabetic by Family Then by Species	Life Form	Native/ Introduced		ool/Warm Season
URTICACEAE				
Parietaria pensylvanica Muhl. PENNSYLVANIA PELLITORY (PAPE)	F	N	A	С
VERBENACEAE				
Phyla cuneifolia (Torr.) Greene [syn. Lippia cuneifolia (Torr.) Steud.] WEDGELEAF FOGFRUIT (PHCU)	F	N	P	W
Verbena bipinnatifida Nutt. (syn. V. ambrosifolia Rydb.) DAKOTA VERVAIN (VEBI)	F	N	Р	С
Verbena bracteata Lag. & Rodr. PROSTRATE VERVAIN (VEBR)	F	N	A	C
VIOLACEAE				
Viola nuttallii Pursh NUTTALL VIOLET (VINU)	F	N	P	С
VITACEAE				
Parthenocissus vitacea (Knerr) Hitchc. THICKET CREEPER (PAVI1)	V	N	P	С
Vitis longii Prince (syn. V. acerifolia Raf. LONGS GRAPE (VILO)	V	N	P	С

Alphabetic by Family	Life	Native/	Co	ool/Warm
Then by Species	Form	Introduced	Longevity	Season
ZYGOPHYLLACEAE				
Tribulus terrestris L. PUNCTURE VINE (TRTE)	\mathbf{F}	I	A	W

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NEW NAMES AND NEW COMBINATIONS IN THE GENUS EUPHORBIA L. (EUPHORBIACEAE)

Rob C.H.M. Oudejans van Konijnenburglaan 12, 3925 XB Scherpenzeel, The Netherlands

ABSTRACT

New names and combinations are published for *Euphorbia* in anticipation of future publication of a listing of all names applied to the tribe Euphorbieae (Euphorbiaceae).

KEY WORDS: Euphorbiaceae, Euphorbia, nomenclature.

During the preparation of a world list of all species names published in the tribe Euphorbieae (Euphorbiaceae) with their distribution (Oudejans, in preparation), several new names and new combinations appeared to be necessary. The list will contain over 10,000 names, including synonyms, misspellings, etc. Prior to the publication of the list, for better accessibility, all name changes will be published in this paper.

Currently, the tribe contains the following genera: Euphorbia L., Monadenium Pax, Synadenium Boissier, Endadenium Leach, Neoguillauminia Croizat, Pedilanthus Poiteau, Anthostema Adr. Jussieu, Dichostemma Pierre, Calycopeplus Planchon and Cubanthus Millspaugh.

All other genera will be treated in my world list as synonyms or subgenera of the genera mentioned. This holds particularly for Chamaesyce Rafinesque and Tithymalus Gaertner, which are considered as separate genera by several authors (for instance, Soják 1983; Koutnik 1987), whereas others include them in the genus Euphorbia L. (for instance, Radcliffe-Smith 1986; Carter 1988). In my opinion, for stability of nomenclature, the best solution is accepting these names as subgenera, until the tribe Euphorbieae can be studied on a world basis. Most problems of interpretation originate from the vast distribution of the genus Euphorbia L. over all continents with so many pantropic weedy species and different growth forms, resulting in publication of new species and genera on a basis too limited for "correct" concepts accepted universally.

- Euphorbia adenoptera Bertoloni subsp. gundlachii (Urban) Oudejans, comb. nov. Basionym: E. gundlachii I. Urban, Symb. Antill. 5:392-393. 1908.
- Euphorbia adenoptera Bertoloni subsp. pergamena (Small) Oudejans, comb. nov. Basionym: E. pergamena J.K. Small, Bull. Torrey Bot. Club 25:615-616. 1898.
- Euphorbia alainii Oudejans, nom. nov., pro Chamaesyce montana H. Alain [=A.H. Liogier], Moscosoa 1(1):25-26. 1976. The epithet montana is not available in the genus Euphorbia. TYPE: REPUBLICA DOMINICANA. En Pinar, Alto del Toro, Sierra de Bahoruco, 2200 m, Alain & Perfa Liogier 19712.
- Euphorbia amandi Oudejans, nom. nov., pro E. minuta R.A. Philippi, Anales Mus. Nac. Chile (secc. 2, Bot.) 8:76. 1891. TYPE: CHILE. habitat in Tarapacá, de Cacalhuay advecta. Non E. minuta F. Loscos y Bernal & J. Pardo y Sastron, Ser. Inconf. Pl. Arag. 96. 1863.
- Euphorbia antonii Oudejans, nom. nov., pro E. lanceolata D.A. Larrañaga, Escritos D.A. Larrañaga 2:164. 1923. TYPE: [URUGUAY.] Julio 21 de 1809. Non E. lanceolata K.[P.J.] Sprengel, Fl. Halens. Mant. 41-42. 1807.
- Euphorbia barnesii (Millspaugh) Oudejans, comb. nov. Basionym: Adenopetalum barnesii C.F. Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:377. 1913.
- Euphorbia blatteri Oudejans, nom. nov., pro E. helioscopioides E. Blatter, J. Bombay Nat. Hist. Soc. 36:483. 1933. TYPE: S. Waziristan, Sararogha, 4000 ft, Fernandez 105. Non E. helioscopioides F. Loscos y Bernal & J. Pardo y Sastron, Ser. Inconf. Pl. Arag. 93. 1863.
- Euphorbia bruntii (Proctor) Oudejans, comb. nov. Basionym: Chamaesyce bruntii G.R. Proctor, Sloanea 1:2. 1977.
- Euphorbia celastroides Boissier in DC var. tomentella (Boissier in DC) Oudejans, comb. nov. Basionym: E. multiformis Hooker & Arnott var. tomentella [P.]E. Boissier in A.P. de Candolle, Prodr. 15(2):12. 1862.
- Euphorbia chapmanii Oudejans, nom. nov., pro E. nudicaulis A.W. Chapman, Fl. South. U.S. (ed. 1) 402. 1860. TYPE: UNITED STATES. near St. Joseph's, west Florida. Non E. nudicaulis G. Perrottet, Mem. Soc. Linn. Paris 3(1):116. 1826 (also as preprint 1824).
- Euphorbia chiogenes (Small) Oudejans, comb. nov. Basionym: Chamae-syce chiogenes J.K. Small, Fl. Southeast. U.S. 709,1333. 1903.
- Euphorbia conferta (Small) Oudejans, comb. nov. Basionym: Chamaesyce conferta J.K. Small, Fl. Southeast. U.S. 713-714. 1903. Earlier combinations made by B.E. Smith (1946) and E. Jablonski (1974) are invalid.

- Euphorbia cordatella Oudejans, nom. nov., pro E. cordata D.A. Larrañaga, Escritos D.A. Larrañaga 2:164. 1923. TYPE: [URUGUAY.] Abril 5 de 1814. Non E. cordata F. von Paula von Schrank, Baier. Fl. 1:747. 1789.
- Euphorbia cowellii (Millspaugh ex Britton) Oudejans, comb. nov. Basionym: Chamaesyce cowellii [C.F.] Millspaugh ex N.L. Britton, Bull. Torrey Bot. Club 43:457. 1916.
- Euphorbia cumulicola (Small) Oudejans, comb. nov. Basionym: Chamaesyce cumulicola J.K. Small, Man. Southeast. Fl. 794,1505. 1933.
- Euphorbia damasoi Oudejans, nom. nov, pro E. ovata D.A. Larrañaga, Escritos Larrañaga, 2:164. 1923. TYPE: URUGUAY. Feb 25 de 1812. Non E. ovata E. Meyer ex [P.]E. Boissier in A.P. de Candolle, Prodr. 15(2):167. 1862.
- Euphorbia deltoidea Engelmann ex Chapman var. serpyllum (Small) Oudejans, comb. nov. Basionym: *Chamaesyce serpyllum* J.K. Small, Fl. Florida Keys 81. 1913.
- Euphorbia denisii Oudejans, nom. nov., pro E. obcordata M. Denis, Euphorb. Iles Austr. Afr. 56. 1921. TYPE: MADAGASCAR. Région de Sud-Ouest, bassin de l'Onilany, Perrier de la Bâthie 9785. Non E. obcordata [I.]B. Balfour, Proc. Roy. Soc. Edinburgh 12:93. 1882-1883.
- Euphorbia donii Oudejans, nom. nov., pro E. longifolia D. Don, Prodr. Fl. Nepal 62. 1825. TYPE: hab. in Nepalia, Hamilton [s.n.]. Non E. longifolia J.B.A.P.M. de Lamarck, Encycl. 2:417. 1788.
- Euphorbia dubovikii Oudejans, nom. nov., pro E. pinetorum Dubovik ex O.N. Dubovik & M.V. Klokov, Novosti Sist. Vyssh. Inzsh. Rast. (Kiev) 1976:105-107. 1977. TYPE: Dit. Krasnodarensis, prope Gelendzhik, p. Archipo-Ossipovka, O. Dubovik [s.n.]. Non E. pinetorum (Small) G.L. Webster, J. Arnold Arbor. 48:403. 1967.
- Euphorbia duckei (Croizat) Oudejans, comb. nov. Basionym: Chamaesyce duckei L. Croizat, J. Arnold Arbor. 24:185-186. 1943.
- Euphorbia georgei Oudejans, nom. nov., pro E. acuta G. Engelmann in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):189. 1858. TYPE: UNITED STATES. Texas: stony prairies western Texas, along the San Pecos rivers, &c. Bigelow [s.n.], Schott [s.n.], Wright 1739,1749. Non E. acuta Bellard ex A. Colla, Herb. Pedem. 5:132. 1836.
- Euphorbia graminifolia Villars subsp. tommasiniana (Bertoloni) Oudejans, comb. nov. Basionym: E. tommasiniana A. Bertoloni, Fl. Ital. 5(1):78-79. 1842.
- Euphorbia graminifolia Villars subsp. zhiguliensis (Prokhanov) Oudejans, comb. nov. Basionym: Galarrhoeus ('Galarhoeus') zhiguliensis Ya.I. Prokhanov, Tr. Kuibyshevsk. Bot. Sada 1:64-68. 1941.

- Euphorbia hamiltonii Oudejans, nom. nov., pro E. angustifolia Hamilton ex D. Don, Prodr. Fl. Nepal 62. 1825. TYPE: hab. ad Norcotera Nepalensium, Hamilton [s.n.]. Non E. angustifolia (Haworth) E.G. von Steudel, Nomencl. (ed. 1) 323. 1821.
- Euphorbia heraldiana (Millspaugh) Oudejans, comb. nov. Basionym: Chamaesyce heraldiana C.F. Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:409. 1916.
- Euphorbia herbstii (Wagner) Oudejans, comb. nov. Basionym: Chamae-syce herbstii W.L. Wagner, Bishop Mus. Occas. Pap. 28:75-76. 1988.
- Euphorbia hiernii (Croizat) Oudejans, comb. nov. Basionym: Elaeophorbia hiernii L. Croizat, Desert Pl. Life 8:102-103. 1936.
- Euphorbia hurusawae Oudejans, nom. rov., pro E. barbellata I. Hurusawa, J. Jap. Bot. 16:571-572. 1940. TYPE: CHINA. hab. in Manshuria, prov. Kwantung, in monte Dai-osyo-zan, M. Nishimura [s.n.]. Non E. barbellata G. Engelmann in W.H. Emery, Rep. U.S. Mex. Bound. 2(1):190. 1858.
- Euphorbia hurusawae Oudejans var. imaii (Hurusawa) Oudejans, comb. nov. Basionym: E. imaii I. Hurusawa. J. Jap. Bot. 16:576-577. 1940.
- Euphorbia inaguaensis Oudejans, nom. nov., pro E. abbreviata D.S. Correll, Sida 8(4):317-319. 1980. TYPE: BAHAMA ISLANDS. Little Inagua, D.S. Correll 45998. Non E. abbreviata J.L. Thuillier, Fl. Paris (ed. 2) 239. 1799.
- Euphorbia josei Oudejans, nom. nov., pro E. litoralis M. [de] Sessé [y Lacasta] & J.M. Moçiño, Fl. Mexic. (ed. 2) 123. 1894. TYPE: habitat ad litora maris insulae de Puerto Rico. Non E. litoralis C.S. Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 2:54. 1817.
- Euphorbia klotzschii Oudejans, nom. nov., pro E. ovalifolia (Engelmann ex Klotzsch) [P.]E. Boissier in A.P. de Candolle, Prodr. 15(2):43. 1862. TYPE: CHILE: hab. in Chili prope Santiago [Santjago] et Atacama, Philippi [s.n.]. Non E. ovalifolia V.F. Kosteletzky, Allg. Med. Pharm. Fl. 5:1724. 1836.
- Euphorbia larranagae Oudejans, nom. nov., pro E. rupestris D.A. Larra ñaga, Escritos D.A. Larrañaga 2:164. 1923. TYPE: [Uruguay]. Non E. rupestris C.A. Meyer ex C.F. Ledebour, Icon. Pl. Fl. Ross. 2:26. 1830.
- Euphorbia leoncroizatii Oudejans, nom. nov., pro E. croizatii (Hurusawa) M. Kitagawa, J. Jap. Bot. 31:304 (as 'Croizatii'). 1956. TYPE: CHINA: hab. Manschuria, prov. Fengtien. Non E. croizatii J. Leandri, Notulae Syst. 12:160-161 (as 'Croizati'). 1946

- Euphorbia limaensis Oudejans, nom. nov., pro E. inornata (Dressler) A. Radcliffe-Smith, Kew Bull. 32:482. 1978. TYPE: PERÚ. Dept. & Prov. Lima, Distr. Pachacamac, Atacongo, 195 m, Ynes Mexia 04044. Non E. inornata N.E. Brown in W.T. Thiselton-Dyer, Fl. Cap. 5(2):585. 1925.
- Euphorbia lutulenta (Croizat) Oudejans, comb. nov. Basionym Chamaesyce lutulenta Croizat, J. Arnold Arbor. 26:195-196. 1945.
- Euphorbia marianoi Oudejans, nom. nov., pro E. pulchella M. [de] Sessé [y Lacasta] & J.M. Moçiño, Pl. Nov. Hisp. (ed. I) 81. 1888 ('1887').
 TYPE: [MÉXICO?]. habitat in oppidis Ario et Uruapum. Non E. pulchella M. Lagasca [y Segura] & J. Rodriguez, Anales Cienc. Nat. (Madrid) 5:71-72. 1802.
- Euphorbia mazatlamensis Oudejans, nom. nov., pro E. triflora M. [de]
 Sessé [y Lacasta] & J.M. Moçiño, Pl. Nov. Hisp. (ed. 1) 81. 1888 ('1887').
 TYPE: MÉXICO. habitat in Mazatlam. Non E. triflora H. Schott, C.F.
 Nyman & Th. Kotschy, Analecta Bot. 63-64. 1854.
- Euphorbia mocinoi Oudejans, nom. nov., pro E. peltata M. [de] Sessé [y Lacasta] & J.M. Moçiño, Fl. Mexic. (ed. 2) 122. 1894. TYPE: MÉXICO. habitat in Oppido Nandio, prope Zitacuarum. Non E. peltata W. Roxburgh, Fl. Ind. (ed. 2) 2:474. 1832.
- Euphorbia nicaeensis Allioni subsp. maleevii (Tamamshyan) Oudejans, comb. nov. Basionym: E. maleevii S.G. Tamamshyan, Dokl. Akad. Nauk Armyansk. SSR 1(1-2):45-46 (as 'Maleevi). 1944.
- Euphorbia nicholasii Oudejans, nom. nov., pro Elaeophorbia acuta N.E. Brown in W.T. Thiselton-Dyer, Fl. Cap. 5(2):222. 1915. TYPE: SOUTH AFRICA. probably the Transvaal, Burtt-Davy [s.n.]. The name acuta is not available in the genus Euphorbia.
- Euphorbia ocellata Durand & Hilgard subsp. arenicola (Parish) Oudejans, comb. nov. Basionym: E. arenicola S.B. Parish, Erythea 7:93. 1899.
- Euphorbia ocellata Durand & Hilgard subsp. rattanii (Watson) Oudejans, comb. nov. Basionym: E. rattanii S. Watson, Proc. Amer. Acad. Arts Sci. 20:372. 1885.
- Euphorbia orbifolia (Alain) Oudejans, comb. nov. Basionym: Chamae-syce orbifolia H. Alain [=A.H. Liogier], Phytologia 47:175-177. 1980.
- Euphorbia paredonensis (Millspaugh) Oudejans, comb. nov. Basionym: Chamaesyce paredonensis C.F. Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:393-394. 1914.
- Euphorbia parodii Oudejans, nom. nov., pro E. angustifolia D. Parodi, Anales Soc. Cient. Argent. 11:49-50 (as augustifolia). 1881. TYPE: PARAGUAY. Igatimi in pratis. Non E. angustifolia (Haworth) E.G. von Steudel, Nomencl. (ed. 1) 323. 1821.

- Euphorbia porteriana (Small) Oudejans, comb. nov. Basionym: Chamaesyce porteriana J.K. Small, Fl. Southeast. U.S. 711-712,1333. 1903.
- Euphorbia porteriana (Small) Oudejans var. keyensis (Small) Oudejans, comb. nov. Basionym: *Chamaesyce keyensis* J.K. Small, Torreya 28:6. 1928.
- Euphorbia porteriana (Small) Oudejans var. scoparia (Small) Oudejans, comb. nov. Basionym: Chamaesyce scoparia J.K. Small, Fl. Florida Keys 81. 1913.
- Euphorbia radlkoferi Oudejans, nom. nov., pro E. gracilis L.[A.] Radl-kofer, Leafl. Philipp. Bot. 5(Art. 79):1606-1607. 1913. TYPE: PHILIPPINES. in Philippinarum insula Mindanao, Prov. Agusan, Cabadbaran, Mount Urdaneta, 4000 ped, A.D.E. Elmer 13482. Non E. gracilis J.L.A. Loiseleur-Deslongchamps, Fl. Gall. (ed. 1) 2:728. 1807.
- Euphorbia raphilippii Oudejans, nom. nov., pro E. lanceolata R.A. Philippi, Anales Univ. Santiago 91:508. 1895. TYPE: [CHILE.] Habitat in Andibus Illapelinis loco dicto el Peñoa. Non E. lanceolata K.[P.J.] Sprengel, Fl. Halens. Mant. 41-42. 1807.
- Euphorbia rochaensis (Croizat) Oudejans, comb. nov. Basionym: Chamaesyce rochaensis L. Croizat, J. Arnold Arbor. 26:195. 1945.
- Euphorbia rockii Forbes var. grandiflora (Hillebrand) Oudejans, comb. nov. Basionym: E. clusiifolia var. grandiflora W. Hillebrand, Fl. Hawaiian Isl. 395 (as 'clusiaefolia'). 1888.
- Euphorbia roschianica (Ikonnikov) Oudejans, comb. nov. Basionym: *Tithymalus roschianicus* S.S. Ikonnikov, Novosti Sist. Vyssh. Rast. 15:220-221. 1979.
- Euphorbia rothrockii (Millspaugh) Oudejans, comb. nov. Basionym: Chamaesyce rothrockii C.F. Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:376-377. 1913.
- Euphorbia serpyllifolia Persoon subsp. hirtula (Engelmann ex Watson) Oudejans, comb. nov. Basionym: E. hirtula [G.] Engelmann ex S. Watson, Bot. Calif. 2:74. 1880.
- Euphorbia sessei Oudejans, nom. nov., pro E. imbricata M. [de] Sessé [y Lacasta] & J.M. Moçiño, Fl. Mexic. (ed. 2) 123. 1894. TYPE: habitat ad litore maris prope Havanam. Non E. imbricata M. Vahl, Symb. Bot. 2:54-55. 1791.
- Euphorbia smallii Oudejans, nom. nov., pro Chamaesyce pinetorum J.K. Small, Bull. N.Y. Bot. Gard. 3:429-430. TYPE: UNITED STATES. [Florida:] between Cutler and Camp Longview Small & Carter 836. The name pinetorum is not available in the genus Euphorbia.

- Euphorbia standleyi (Millspaugh) Oudejans, comb. nov. Basionym: Chamaesyce standleyi C.F. Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:404. 1916.
- Euphorbia tamaulipasana (Millspaugh) Oudejans, comb. nov. Basionym: Chamaesyce tamaulipasana C.F. Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:403-404. 1916.
- Euphorbia triphylla (Klotzsch & Garcke ex Klotzsch) Oudejans, comb. nov. Basionym: Eumecanthus triphyllus Klotzsch & Garcke ex J.F. Klotzsch, Abh. K. Akad. Wiss. Berlin 1859(1):43. 1860.
- Euphorbia urbanii (Millspaugh) Oudejans, comb. nov. Basionym: Chamaesyce urbanii Millspaugh, Field Mus. Nat. Hist., Bot. Ser. 2:412. 1916.
- Euphorbia waldsteinii (Soják) Radcliffe-Smith subsp. jaxartica (Prokhanov) Oudejans, comb. nov. Basionym: Tithymalus jaxarticus Ya.I. Prokhanov, Consp. Syst. Tithym. As. Med. 192-197. 1933.
- Euphorbia wangii Oudejans, nom. nov., pro E. villifera Wentsai [=W.T.] Wang, Acta Bot. Yunnanica 10(1):42. 1988. TYPE: CHINA. Gansu: Zhouqiu, alt. 2000 m, 20 Maj 1959, Jiang Shu & Jin Cun-li 361. Non E. villifera A. Scheele, Linnaea 22:153-154. 1849.
- Euphorbia wootonii Oudejans, nom. nov., pro Zygophyllidium delicatulum E.O. Wooton & P.C. Standley, Contrib. U.S. Natl. Herb. 16(4):145. 1913. TYPE: UNITED STATES. [New Mexico:] Sierra County, Mineral Creek, 2250 m, O.B. Metcalfe 1414. The name delicatula is not available in the genus Euphorbia.

LITERATURE CITED

- Carter, S. 1988. Flora of Tropical East Africa (R.M. Polhill, ed.). Euphorbiaceae (part 2), tribe Euphorbieae.
- Koutnik, D.L. 1987. A taxonomic revision of the Hawaiian species of the genus Chamaesyce (Euphorbiaceae). Allertonia 4(6):331-388.
- Radcliffe-Smith, A. 1986. Flora of Pakistan (E. Nasir & S.I. Ali, eds.). Euphorbiaceae.
- Soják, J. 1983. Fragmenta phytotaxonomica et nomenclatorica (4). Cas. Nar. Muz. 152(1):12-25.

EFFECTS OF METOLACHLOR AND ALACHLOR ON PERMEABILITY AND LIPID SYNTHESIS IN SOME PLANTS

M. Kord¹ & T. Hathout²

¹ Botany Department, Faculty of Science, Cairo University, Cairo, EGYPT
² Botany Department, Girls College, Ain Shams University, Cairo, EGYPT

ABSTRACT

This study was carried out to investigate the effects of metolachlor on root permeability and to determine whether metolachlor or alachlor inhibit plant lipid synthesis.

Metolachlor at 30 and 40 ppm increased the leakage of previously absorbed ³²P-labelled orthophosphate from the roots of onion (a susceptible species) by 14 and 41 times the control values respectively. A significant amount of ³²P leaked from the roots of the moderately susceptible species (wheat and tomato) whereas no significant loss of ³²P occurred to two tolerant species (*Pisum* and corn). At 10 or 20 ppm, 1,8-naphthalic anhydride prevented ³²P leakage from onion roots in the presence of 30 ppm metolachlor. High concentrations of naphthalic anhydride, however, promoted ³²P leakage and did not protect onion roots from the leakage induced by high concentrations (40 ppm) of metolachlor. Neither metolachlor nor alachlor at 40 ppm, inhibited the uptake of acetate-2-¹⁴C or malonic acid-2-¹⁴C into excised wheat root tips.

Incorporation of ¹⁴C-choline chloride into phosphatidylcholine was not significantly inhibited by metolachlor.

KEY WORDS: Plant physiology, metolachlor, alachlor, radioactive labeling.

INTRODUCTION

Metolachlor is a selective herbicide used for the control of grass weeds, nutsedge and broadleaf species in corn. Other crops showing tolerance include soybean, peanut, potato and certain vegetables.

Numerous studies have been conducted to determine the mechanism of action of α -chloroacetamides. Studies of photosynthesis, respiration, α -amylase

synthesis, RNA synthesis, protein synthesis and lipid synthesis have failed, however, to elucidate the primary mechanism of action (Chandler et al. 1972; Devlin & Cunningham 1970; Diner et al. 1978; Duke et al. 1975; Jaworski 1956; Moreland et al. 1969; Sasaki et al. 1966 and Truelove & Diner 1978).

There is a considerable literature on the effects of metolachlor on the morphology of higher plants.

Dixon (1981), came to the conclusion that 100 ppm of metolachlor reduced shoot growth of maize by 65%, and the uptake of the herbicide was twice in maize as in nutsedge.

Shoot and root growth are inhibited by α -chloroacetamides (Deal & Hess 1980; Duke et al. 1975; Keeley et al. 1972 and Pillai et al. 1979). Deal & Hess (1980), found that growth of *Pisum sativum* and *Avena sativa* were inhibited by both metolachlor and alachlor. They suggested that growth inhibition by these herbicides resulted from an inhibition of both cell division and cell enlargement.

Protein synthesis is inhibited by the effect of certain α -chloroacetamides (Mann et al. 1965). Pillai et al. (1979), found that, with metolachlor, leucine incorporation into protein was inhibited only at concentrations of 1 x 10^{-4} M and higher.

Diner et al. (1978), found that α -amylase synthesis was inhibited by alachlor and metolachlor only at concentrations in excess of 1 x 10⁻³M.

While conducting studies on the effects of α -chloroacetamides on root growth, the nutrient solution containing 40 ppm metolachlor (where the onion roots were growing) became turbid after 48 hrs and extensive colonies of fungi and bacteria were associated with the roots. This observation suggested the possibility that the herbicide was stimulating the growth of these organisms by causing the leakage of substance from the roots that stimulated microbial growth. This further suggested that the herbicide may be causing a loss of root cell membrane integrity.

Studies of the interaction between herbicide and lipids (one of the two major components of cell membrane) have been carried out by Mann & Pu (1968). Using excised hypocotyls of Hemp sesbania, they demonstrated that a number of herbicides, including the α -chloroacetamide can inhibit lipoxygenases as measured by a reduction in the incorporation of malonic acid-2-¹⁻¹C into lipid.

MATERIALS AND METHODS

Seeds of Allium cepa L. purchased from The Ministry of Agriculture, Cairo, were surface sterilized, and their basal ends were submerged in beakers containing half-strength nutrient solution (Hoagland & Arnon 1950). Roots were allowed to grow for 10 days at 27°C and constant light intensity of about (6,000 lux) in a growth chamber. Nine onions with a similar number of roots

were transferred to beakers containing 60 ml of phosphorus deficient, half strength nutrient solution containing 5 μ Ci 32 P as orthophosphate (sp. act. 0.8 mCi/ml). The bulbs were placed so that only the roots were in contact with the radioactive solution. After 24 hrs, onions were removed from the 32 P solution and the roots were washed three times with fresh nutrient solution before transferring them to beakers containing 60 ml of half strength nutrient solution, which contained 100 μ g/ml penicillin and 40 μ g/ml chloramphenicol to inhibit microbial growth. A stock solution of metolachlor in ethanol was added to give final concentrations of 0, 30 or 40 ppm herbicide in each of three replications. A similar amount of ethanol was present in the no-herbicide controls. Duplicate 0.2 ml samples of the solutions were withdrawn after 0, 4, 8 and 12 hrs and then every 12 hrs for 6 days. These samples were radio assayed by Packard liquid scintillation, type spectrometer series 4000.

Similar studies were conducted using roots of Lycopersicon lycopersicum L., Zea mays L., Triticum aestivum L. and Pisum sativum L.

To show the effect of naphthalic anhydride on metolachlor-induced ³²P leakage from onion roots, the experiments were conducted as described above, but naphthalic anhydride was added to some of the treatments. Preliminary experiments were carried out using aqueous naphthalic anhydride suspensions containing 0.1 and 0.4% respectively, applied both alone and with 40 ppm metolachlor. Later experiments used lower rates of both 10, 20 and 30 ppm metolachlor.

Wheat grains were germinated for 72 hrs in the dark at 28°C on filter paper moistened with 1 x 10^{-3} M CaCl₂. After harvesting, 1 cm long root tips were excised and held in cold aqueous sucrose until a sufficient number had been collected. Groups of 100 root tips were removed from the sucrose and transferred to flasks containing 2 ml of 0.01 M potassium phosphate, 1% sucrose and 10 μ g/ml chloramphenicol. Herbicide, dissolved in ethanol, was added to give a final herbicide concentration of 40 ppm. Ethanol was present in all treatments at a concentration of 0.5%, 5 microcuries of malonic acid-2-¹⁴C (sp. act. 50.4 mCi/ml) were added as a precursor for lipid synthesis.

Flasks were covered with black polyurethane and the root tips were incubated for 6 hours at 30° C in a shaking water bath. Following incubation, root tips were removed, washed twice with non labeled malonic-acid (200 μ g/ml) and twice with water. The root tips were then frozen at 0° C, freeze dried and weighed before grinding in a mortar. The tissue was transferred into 20 ml of chloroform:methanol (2:1) mechanically stirred for one hour and filtered through a double thickness Whatman No. 1 filter paper.

The filtrate was dried under a stream of N₂. The crude lipid extract was dissolved in 5 ml chloroform, 2 ml H₂0 was added, and the mixture was shaken. The lower chloroform layer was removed and passed through a small glass column containing anhydrous sodium sulfate to remove residual water

and water soluble non lipid residues. This fraction and the upper, aqueous layer (non incorporated precursor) were both sampled and radio assayed by liquid scintillation.

Further studies were conducted in the same manner, but using acetate-2-11C (sp. act. 59.2 mCi/ml) as lipid precursor instead of malonic acid-2-11C. Similar studies were conducted using a longer incubation period of nine hours. Lipid extracts were spotted on pre-coated TLC plates and separated using petroleum ether:diethyl ether:acetic acid (79:10:1).

Radioactive areas were detected by scanning the plate with a TLC radioscanner. The phospholipids, which remained on the TLC plates, were extracted from the silica gel with chloroform:methanol:water (5:5:1). Extracts were dried under N₂ and redissolved in chloroform prior to further separation by TLC. The remaining lipid classes on the TLC plates were removed by scraping the radioactive areas of silica gel into vials containing scintillation fluid. The vials were then assayed by liquid scintillation.

To study the incorporation of choline chloride into phosphatidylcholine, the experiments were carried out in a similar way to malonic acid-2- 14 C and acetate-2- 14 C incorporation studies with the following exceptions 1.0 μ Ci choline chloride-1-2- 14 C (sp. act. 5.4 mCi/ml) was used as a precursor to phosphatidylcholine and the preliminary TLC of the lipid extract to separate the neutral lipids from the polar phospholipids was omitted. Radioactivity remaining at the origin of the TLC plate after separation by polar solvent system was eluted, concentrated and identified as choline chloride using paper chromatography and a solvent system of n-butanol:ethanol:acetic acid:water (8:2:1:3).

RESULTS AND DISCUSSION

Preliminary studies with onion had suggested that metolachlor was affecting the permeability of root membranes, causing leakage of plant metabolites.

To determine whether the effects of metolachlor on permeability were related to the phytotoxicity range of the herbicide, several species differing in sensitivity to metolachlor were tested (Figure 1). In the absence of herbicide, there was very little leakage of ³²P from the roots of any of the species, indicating that the antibiotic and alcohol in the nutrient solutions had little if any effect on root permeability. Neither herbicide treated Zea nor Pisum (both metolachlor tolerant species) showed any significant leakage of ³²P from the roots compared to untreated plants, even at an herbicide concentration of 40 ppm. The two moderately susceptible species (tomato and wheat) showed three and four times the untreated plant level of ³²P leakage respectively, after 144 hours treatment with 30 ppm metolachlor. In the presence of 40 ppm metolachlor, however, ³²P leakage from these two species was 14 and 11 times the control rates respectively.

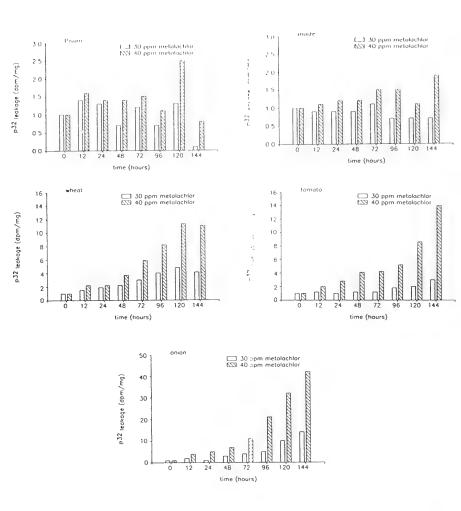


Figure 1. The effect of metolachlor on the leakage of previously absorbed $^{32}\mathrm{P}$ from roots of five plants.

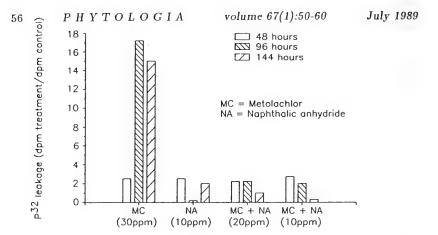
The maximum leakage of previously absorbed \$^{32}P\$ was from the roots of onion, a species highly sensitive to metolachlor. At 30 ppm metolachlor, \$^{32}P\$ leakage from onion roots was 14 times that of untreated roots after 144 hours. At 40 ppm metolachlor, \$^{32}P\$ leakage was 41 times the control value. Leakage of \$^{32}P\$ by onion roots was significantly different from the control after 72 hours with the 40 ppm metolachlor concentration. At its most extreme, the amount of \$^{32}P\$ released from herbicide treated onion roots was about 10% of the total amount absorbed. Because \$^{32}P\$ absorbed by roots is rapidly translocated to the shoot system, however, the amount lost would represent considerably more than 10% of the \$^{32}P\$ remaining in the roots. The reason for the differing rates of \$^{32}P\$ leakage, however, is not known. From these studies, it was not possible to determine whether metolachlor was exerting a direct effect on root membranes, or whether the leakage of exudates was a secondary effect resulting from an inhibition by the herbicide of some metabolic process related to membrane function or to the maintenance of membrane integrity.

Seed protectants can confer on germinating seeds a higher tolerance to herbicides and thus widen the margins of safety and selectivity. The potential of using naphthalic anhydride as a safener against metolachlor and alachlor injury has been tested, and it has been shown that naphthalic anhydride can prevent herbicide injury from these herbicides in sorghum (Ahrens & Davis 1978; Jordan & Jolliffe 1971 and Truelove & Davis 1977) and against alachlor injury to Zea (Burnside et al. 1971). These studies were conducted to determine whether naphthalic anhydride could protect onion roots from the permeability changes induced by metolachlor. The results are shown in Figure 2.

Metolachlor at a concentration of 30 ppm applied to onion roots via nutrient solution caused a 15 fold increase in the leakage of ³²P after 144 hours of treatment (Figure 2). When naphthalic anhydride at either 10 or 20 ppm was applied to onion roots with metolachlor at a concentration 30 ppm, however, very little ³²P leakage occurred. Thus, naphthalic anhydride protected the onion roots against permeability changes induced by metolachlor. Although the mechanism of action of metolachlor is unknown, the studies indicate that leakage of plant nutrients and loss of root cell membrane integrity are probably important factors in the mode of action of this herbicide.

Naphthalic anhydride applied alone at concentrations of 10 ppm did not cause leakage of ³²P from the roots. However, at high rates of application, naphthalic anhydride caused leakage of previously absorbed ³²P from onion roots. Such high rates of naphthalic anhydride did not protect onion roots from leakage induced by metolachlor. In fact, they promoted additional leakage.

St. John & Hilton (1973), reported the efflux of electrolytes from roots of wheat seedlings treated with 1 x 10^{-4} M dinoseb. They found that herbi-



TREATMENT
Figure 2. The effect of 1,8-naphthalic anhydride on metolachlor induced

32P leakage from the roots of onion.

cide treatment reduced polar lipid levels by 72% and suggested that dinoseb may act by decreasing the levels of polar lipids required for membrane formation, hence altering membrane structure and function. Alteration of root membrane permeability characteristics, as shown by the leakage of plant exudates, suggested to us that metolachlor might also be acting through some effect on those metabolic processes involving membrane lipids. The effects of metolachlor and alachlor on lipid synthesis were determined by following the uptake and incorporation of radio labeled precursors into the lipids of excised wheat root tips. The uptake of the precursor, acetate-2-11°C, by both treated and untreated root tips was much greater than that of malonic acid-2-11°C (Figure 3). Between 56 and 63% of the applied acetate-2-11°C was absorbed by excised root tips, but only 7 to 9% of the applied malonic acid-2-11°C was absorbed. Neither alachlor nor metolachlor, however, affected the uptake of either of these precursors.

The radioactivity of the total lipid fraction extracted from herbicide treated tissue was not significantly different from that of untreated tissue, irrespective of which ¹⁴C-labeled precursor was used in the study (Figure 3). The amount of radioactivity incorporated into the lipids, however, differed with the precursor used, with 7 to 9% of the applied acetate-2-¹⁴C and 0.6 to 0.8% of the applied malonic acid-2-¹⁴C incorporated into the lipids.

57

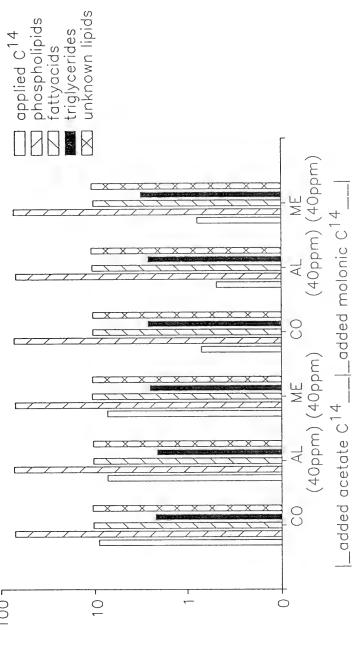


Figure 3. The effects of metolachlor on the incorporation of acetate-2-11C and malonic acid-2-14C into lipids of wheat root tips.

percent

After separation of the total lipid extracts into the constituent lipid classes by TLC, the effect of the herbicide treatment on lipid synthesis could be determined. The incorporation of radio label into the different lipid classes was not inhibited by herbicide treatment. There were no significant differences in either the radio labeled phospholipid fraction or the neutral lipid classes in the total lipid extract.

The phospholipids were eluted from TLC plates and separated into the constituent phospholipid classes by TLC to determine whether alachlor or metolachlor inhibited the synthesis of specific phospholipids. Radio assay indicated that the synthesis of specific phospholipids was not inhibited by either herbicide.

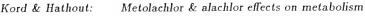
No evidence was found to support the contention that a six hour exposure to alachlor or metolachlor inhibited lipid or phospholipid synthesis in excised wheat root tips.

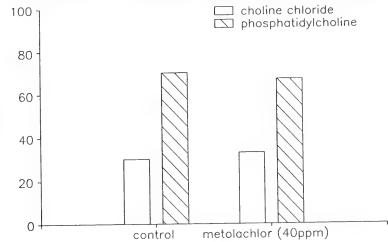
The results of the investigation using a nine hour incubation period were similar to those for the six hour incubation, with no evidence of inhibition of either lipid or phospholipid synthesis by alachlor or metolachlor.

Earlier work had shown significant inhibition of total lipid synthesis by cotton root tips with a metolachlor treatment, although not with an alachlor treatment. More specifically, we had shown that total phospholipid synthesis was inhibited by both metolachlor and alachlor. Wilkinson (1981), failed to confirm these observations and there was no inhibition of lipid or phospholipid by either herbicide in this investigation.

To pursue these investigations further, wheat root tips were incubated with choline chloride-1,2-14C, a precursor for phosphatidylcholine. After separation of the total lipid extract into the constituent lipid classes by TLC, the plates were radio scanned. The scans showed the presence of only two areas of radioactivity on the TLC plates, an area at the origin which accounted for 30% of the total radioactivity, and an area that corresponded to the phospholipid standard, phosphatidylcholine. The radioactivity at the origin was eluted from the silica gel and later identified as choline chloride-1,2¹⁴C by paper chromatography. The results presented in Figure 4 show that the incorporation of choline chloride-1,2-¹⁴C into phosphatidylcholine was not inhibited by metolachlor.

Thus, although metolachlor induces leakage of ³²P from the roots of susceptible species and causes subsequent loss of root cell membrane integrity, we have found no evidence, under these experimental conditions, that this loss of membrane integrity is due to the inhibition of total lipid, phospholipid or phosphatidylcholine synthesis by either alachlor or metolachlor.





percent

Figure 4. The effect of metolachlor on the incorporation of choline chloride 1,2-14C into phosphatidylcholine.

LITERATURE CITED

- Ahrens, W.H. & D.E. Davis. 1978. Seed protectant effects on metolachlor absorption and translocation. Proc. South. Weed Sci. Soc. 31:249.
- Burnside, O.C., G.A. Wicks & E.R. Fenster. 1971. Protecting corn from herbicide injury by seed treatment. Weed Sci. 19:565-568.
- Chandler, J.M., L.M. Croy & P.W. Santlemann. 1972. Alachlor effects on plant nitrogen metabolism and Hill reaction. J. Agric. Food Chem. 20:661-664.
- Deal, L.M. & F.D. Hess. 1980. An analysis of the growth inhibitory characteristics of alachlor and metolachlor. Weed Sci. 28:168-175.
- Devlin, R.M. & R.P. Cunningham. 1970. The inhibition of GA_3 induction of α -amylase activity in barley endosperm by certain herbicides. Weed Res. 10:316-320.
- Diner, A.M., B. Truelove & D.E. Davis. 1978. Metolachlor effects on lipid metabolism in cotton root tips. Proc. South. Weed Sci. Soc. 31:250.
- Dixon, G.A. 1981. Uptake translocation, metabolism, and the effects of metolachlor on yellow nutsedge and corn. (Dissertation Abstracts International, B. 41(11):19-70.
- Duke, W.B., F.W. Slife, J.B. Hanson & H.S. Butler. 1975. An investigation on the mechanism of action of propachlor. Weed Sci. 23:142-147.

- Hoagland, D.R. & D.I. Arnon. 1950. The water-culture method for growing plants without soil. Calif. Agric. Exp. Stn. Circ. #347. 32 pp.
- Jaworski, E.G. 1956. Biochemical action of CDAA, a new herbicide. Science 123:847-848.
- Jordan, L.S. & V.A. Jolliffe. 1971. Protection of plants from herbicides with 1,8-naphthalic anhydride as illustrated with sorghum. Bull. Environ. Contam. Toxicol. 6:417-421.
- Keeley, P.E., C.H. Carter & J.H. Miller. 1972. Evaluation of the relative phytotoxicity of herbicides to cotton and nutsedge. Weed Sci. 20:71-74.
- Mann, J.D., L.S. Jordan & B.E. Day. 1965. A survey of herbicides for their effect upon protein synthesis. Plant Physiol. 40:840-843.
- Mann, J.D. & M. Pu. 1968. Inhibition of lipid synthesis by certain herbicides. Weed Sci. 16:197-198.
- Moreland, D.E., S.S. Malhotra, R.D. Gruenhagen & E.H. Shokraii. 1969. Effects of herbicides on RNA and protein synthesis. Weed Sci. 17:556-563.
- Pillai, P., D.E. Davis & B. Truelove. 1979. Effects of metolachlor on germination, growth, leucine uptake, and protein synthesis. Weed Sci. 27:634-637.
- Sasaki, S. & T.T. Kozlowski. 1966. Influence of herbicides on respiration in young *Pinus* seedlings. Nature (London) 210:439-440.
- St. John, J.B. & J.L. Hilton. 1973. Lipid metabolism as a site of herbicide action. Weed Sci. 21:477-480.
- Truelove, B. & D.E. Davis. 1977. A herbicide antidote seed treatment with naphthalic anhydride. Proc. South. Weed Sci. Soc. 30:364.
- Truelove, B. & A.M. Diner. 1978. Some effects of metolachlor on plant metabolism. Abstr., Weed Sci. Soc. Am. p. 68.
- Wilkinson, R.E. 1981. Influence of metolachlor on phospholipid synthesis in cotton, soybean and sorghum. Proc. South. Weed Sci. Soc. 34:263.

THE SEPARATION OF TRIMORPHA (COMPOSITAE: ASTEREAE) FROM ERIGERON

Guy L. Nesom Department of Botany, University of Texas, Austin, Texas 78713 USA

ABSTRACT

The genus Trimorpha Cass. (Erigeron sect. Trimorpha) is resegregated from Erigeron. The filiform, eligulate pistillate florets and mature pappus that lengthens past the involucre in Trimorpha are not found in Erigeron. Also, the outer phyllaries with three, orange nerves, which are characteristic of Trimorpha, are known in Erigeron in only the three species of sect. Spinosi. In these features of the flowers, pappus and phyllaries, Trimorpha is more similar and apparently more closely related to Conyza than to Erigeron. Six new combinations to Trimorpha are proposed to accommodate the American taxa: T. acris var. asteroides, T. a. var. debilis, T. a. var. kamtschatica, T. elata, T. lonchophylla and T. scotteri.

KEY WORDS: Trimorpha, Erigeron, Asteraceae, New World, systematics.

Erigeron sect. Trimorpha (Cass.) DC. includes a group of species set apart from the rest of the genus by the production of two zones of pistillate flowers, an inner zone of ca 1-4 series of eligulate flowers and an outer of 1-3 series of very numerous flowers with short, narrow, often filiform ligules. Cronquist (1943, p. 629) saw sect. Trimorpha as "inextricably bound to Erigeron ... by the obvious evolutionary line of E. simplex Greene, E. uniflorus L. (sensu lat.) and E. alpinus L., in which E. simplex is true Erigeron, E. alpinus is Trimorpha, and E. uniflorus is somewhat intermediate." In my view, however, E. uniflorus is not intermediate between Trimorpha and true Erigeron, as discussed below, and the two groups are best regarded as different genera.

Trimorpha is distinguished most conspicuously from all of Erigeron by its dimorphic pistillate flowers. At least in some species of Trimorpha, the ligules loosely coil at maturity. The plants are mostly perennials from short, fibrous-rooted rhizomes and produce few-flowered capitulescences that vary from loosely cylindrical panicles or racemes to corymbs. In a few species the heads are solitary. The leaves are entire and buds erect. The outer phyllaries

have three orange-resinous veins, a feature characteristic of Conyza (sensu Nesom [in press]) but found in Erigeron only in the three species of sect. Spinosi (Nesom 1989) and a few others in scattered groups. This feature of nervation is sometimes difficult to observe if the phyllaries are dark-colored, but it is distinctive and occurs in every species of Trimorpha that I have studied. The pappus in plants of Trimorpha also resembles that of Conyza in becoming prominently longer at maturity than the involucre, a feature diagnostic of Conyza but not found in Erigeron.

Erigeron lonchophyllus is a fibrous-rooted annual and, alone in Trimorpha, has only a zone of ligulate, pistillate flowers, lacking the inner zone of eligulate flowers. It clearly belongs with Trimorpha, however, on the basis of its 3-nerved outer phyllaries and elongated pappus. Because of its relatively specialized habit and duration, I believe the lack of the eligulate flowers is a specialization, reflecting a loss rather than a primitive similarity with true Erigeron.

With regard to Cronquist's assertion that Erigeron uniflorus, the generitype of Erigeron (Nesom 1989), occupies an intermediate position between Erigeron and Trimorpha, I find that the putative intermediacy of E. uniflorus lies only in its narrow ligules. In contrast, the ligules do not coil, the outer phyllaries are 1-nerved, and the pappus does not elongate at maturity, features that clearly link it with Erigeron rather than Trimorpha.

Trimorpha, then, differs from Erigeron in several characters, and in these same characters it is similar to Conyza. In my opinion, it is set apart as a genus from Erigeron with at least as much justification as Conyza and appears to be more closely related to Conyza.

Cronquist (1943, p. 631) noted that "In surveying the numerous species which link true Erigeron to true Conyza, we find that in only one place is there any suggestion of a real break. That is between Trimorphaea and Coenotus." With Cronquist, I regard Caenotus as true Conyza (Nesom [in press]). Cronquist also noted (1943, p. 630) that "The differences between Coenotus and Trimorphaea are not great, but the species of the two groups do not seem intimately related. Erigeron canadensis, the most nearly bridging species of the section [Coenotus], is scarcely confusable with any species of Trimorphaea." The morphologically distinct zones of pistillate flowers are not known from any species of Conyza. In addition to this difference, Conyza is a genus primarily of the southern hemisphere, though some of its species are more widespread; Trimorpha is confined to arctic-alpine or temperate regions of the northern hemisphere, and several species are circumboreal.

An alternative taxonomic treatment of Trimorpha would be to recognize it as a well-defined section of Conyza. This would emphasize its similarity to Conyza but would require a much greater number of nomenclatural combinations than the approach taken here, since at least 40 of the Old World

taxa already have names as Trimorpha.

TRIMORPHA Cass., Bull. Sci. Soc. Philom. Paris 1817:137. 1817. TYPE: Trimorpha vulgaris Cass. in Cuvier, Dict. Sci. Nat. 55:324. 1828 (=E. acris L.). Trimorphaea Cass. in Cuvier, Dict. Sci. Nat. 37:462. 1825. Erigeron sect. Trimorpha (Cass. in F. Cuvier) DC., Prodr. 5:290. 1836. Erigeron subg. Trimorpha (Cass.) M. Popov, Acta Inst. Bot. Acad. Sci. URSS, Ser. 1, Fasc. 7:10. 1948.

In the original publication of the genus Trimorpha (1817), Cassini cited Erigeron acris L. as its sole constituent. Not until 1828 did he name a species in the former genus, and there he cited E. acris as a synonym of T. vulgaris. In 1825, Cassini began using the orthographical variant Trimorphaea, listing the original Trimorpha as a synonym. I have discussed other aspects of the lectotypification of Erigeron and Trimorpha in a separate paper (Nesom 1989).

- Trimorpha sect. Brachyglossae Vierh., Beih. Bot. Centralbl. 19:423. 1906. LECTOTYPE (designated here): T. acris (L.) S.F. Gray (=Erigeron acris L.).
- Trimorpha sect. Macroglossae Vierh., Beih. Bot. Centralbl. 19:424. 1906. LECTOTYPE (designated here): T. alpina (L.) S.F. Gray (=Erigeron alpinus L.).
- Erigeron (sp.-group) Acres Rydb., Fl. Colorado 359.1906, in clave. TYPE: E. acris L.
- Tessenia P. Bubani, Fl. Pyrenaea 2:264. 1899. LECTOTYPE (designated here): Tessenia alpina (L.) P. Bubani (=Erigeron alpinus L.).

Tessenia was a superfluous and substitute name for Erigeron by Bubani. It was later used by Lunnell (1917).

There are about 40-45 North American and Eurasian species in Trimorpha. The whole group is in need of critical taxonomic study. From Eurasia, Vierhapper (1906) treated Trimorpha as a genus and included 26 species; Botschantzev (1959) included 17 species in Trimorpha as a subgenus of Erigeron. In Flora Europaea (Tutin et al., 1976), nine species are treated as Erigeron. From North America, Cronquist (1947) recognized only two species in E. sect. Trimorpha, E. lonchophyllus and E. acris, the latter with several varieties. In his study of the Alaskan flora, where all the American taxa of Trimorpha occur, Hultén (1968b) recognized E. elatus (E. acris var. elatus sensu Cronquist) as a distinct species and added one taxon (E. acris var. kamtschaticus) known from a single collection on the Alaska-Yukon boundary. I propose combinations to Trimorpha for the American taxa as recognized by Hultén, leaving the taxonomy of the Old World species for botanists better acquainted with those species.

NEW WORLD AND CIRCUMBOREAL TAXA

- Trimorpha acris (L.) S.F. Gray, Nat. Arr. Brit. Pl. 2:466. 1821. Erigeron acris L., Sp. Pl. 863. 1753.
- Trimorpha acris var. debilis (A. Gray) Nesom, comb. nov. Erigeron acris var. debilis A. Gray, Syn. Fl. N. Amer. 1(2):220. 1884. Erigeron debilis (A. Gray) Rydb., Mem. N.Y. Bot. Gard. 1:408. 1900.
- Trimorpha acris var. kamtschatica (DC.) Nesom, comb. nov. Erigeron kamtschaticus DC., Prodr. 5:290. 1836. Erigeron acris subsp. kamtschaticus (DC.) Hara, J. Jap. Bot. 15:317. 1939. Erigeron acris var. kamtschaticus (DC.) Herder, Bull. Soc. Nat. Moscou Sect. Biol., Ser. 2. 38:392. 1865.
- Trimorpha acris var. asteroides (Andrz. ex Besser) Nesom, comb. nov. Erigeron asteroides Andrz. ex Besser, Enum. Pl. Volh. 33. 1822.
 Erigeron acris var. asteroides (Andrz. ex Besser) DC., Prodr. 5:290.
 1836. Erigeron politus E. Fries, Summa Veg. Scand. 3:184.1845. Erigeron acris subsp. politus (E. Fries) H. Lindb. f., Enum. Pl. Fennoscand. Orient. 56. 1901; non Schinz & Keller, 1909.

Hultén (1968a) suggested that Erigeron asteroides was not known from America. By the publication of his flora (1968b), however, he had apparently changed his mind, because he included E. acris var. asteroides as a synonym of E. acris subsp. politus.

Trimorpha elata (Hook.) Nesom, comb. nov. Erigeron alpinus γ elatus Hook., Fl. Bor. Amer. 2:18. 1834. Erigeron elatus (Hook.) E. Greene, Pittonia 3:164. 1897. Erigeron acris var. elatus (Hook.) Cronq., Brittonia 6:296. 1947.

I accept Cronquist's argument (1947, p. 297) that Hooker's varietal name is valid and that Greene's name is homotypic and synonymous with it.

- Trimorpha lonchophylla (Hook.) Nesom, comb. nov. Erigeron lonchophyllus Hook., Fl. Bor. Amer. 2:18. 1834.
- Trimorpha scotteri (B. Boivin) Nesom, comb. nov. Erigeron scotteri B.Boivin, Phytologia 23:52. 1972.

According to Boivin (1972), Trimorpha scotteri includes plants that were suggested by Cronquist (1947) to be hybrids between Erigeron humilis Grah. and T. acris var. debilis.

REPRESENTATIVE OLD WORLD TAXA

Trimorpha alpina (L.) S.F. Gray, Nat. Arr. Brit. Pl. 2:467. 1821. Erigeron alpinus L., Sp. Pl. 864. 1753.

- Trimorpha attica (Vill.) Vierh., Beih. Bot. Centralbl. 19:462. 1906. Erigeron atticus Vill., Hist. Pl. Dauph. 3:237. 1788 (incl. E. villarsii Bellardi).
- Trimorpha borealis Vierh., Beih. Bot. Centralbl. 19:447. 1906. Erigeron borealis (Vierh.) Simm., Lunds Univ. Arsskr. n.s. 9:127. 1913.
- Trimorpha epirotica Vierh., Beih. Bot. Centralbl. 19:446. 1906. Erigeron epirotica (Vierh.) Halacsy, Consp. Fl. Graec., Suppl. 53. 1908.
- Trimorpha neglecta (A. Kerner) Vierh., Beih. Bot. Centralbl. 19:451. 1906. Erigeron neglectus A. Kerner, Osterr. Bot. Zeitschr. 21:253. 1871.
- Erigeron orientalis Boiss., Diagn. Pl. Orient. Nov. 3:7. 1856. Apparently no name as Trimorpha.
- Trimorpha podolica (Besser) Vierh., Beih. Bot. Centralbl. 19:423. 1906.

 Erigeron podolicus Besser, Enum. Pl. Volh. 76. 1822.

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LITERATURE CITED

- Boivin, B. 1972. Erigeron. In Flora of the prairie provinces. Phytologia 23:43-55.
- Botschantzev, V.P. 1959. Erigeron. Pp. 191-288 in Flora U.R.S.S., vol. 25, ed. V.L. Komarov. U.S.S.R. Acad. Sciences, Leningrad.
- Cronquist, A. 1943. The separation of *Erigeron* from *Conyza*. Bull. Torrey Bot. Club 70:629-632.
- ______. 1947. Revision of the North American species of Erigeron, north of Mexico. Brittonia 6:121-302.
- Hultén, E. 1968. Comments on the flora of Alaska and Yukon. Arkiv Bot., n. ser. 7:1-147.
- _____. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, California.
- Lunnell, J. 1917. Enumerantur plantae Dakotae septentrionalis vasculares—XII. Amer. Midl. Nat. 5:55-71.

- Nesom, G.L. 1989. Infrageneric taxonomy of New World Erigeron (Compositae: Astereae). Phytologia 67:67-93.
- _____. (in press). Further definition of Conyza (Compositae: Astereae). Phytologia 67:.
- Tutin, T.G. et al. 1976. Erigeron. Pp. 116-120 in Flora Europaea, vol. 4. Cambridge Univ. Press, Cambridge.
- Vierhapper, F. 1906. Monographie der alpinen Erigeron—Arten Europas und Vordasiens. Beih. Bot. Centralbl. 19:385-560.

INFRAGENERIC TAXONOMY OF NEW WORLD ERIGERON (COMPOSITAE: ASTEREAE)

Guy L. Nesom Department of Botany, University of Texas, Austin, Texas 78713 USA

ABSTRACT

In a synopsis of infrageneric taxonomy of New World Erigeron, E. uniflorus L. is accepted as the lectotype of sect. Erigeron; other lectotypes are proposed for a number of sections or generic segregates by G. Don, Nuttall, de Candolle, Rafinesque, Torrey & Gray, Botschantzev and Vierhapper. Eighteen sections, counting sect. Leptostelma of South America, are currently recognized in the New World, eight of which are new: sect. Arenarioides, sect. Imbarba, sect. Cincinnactis, sect. Karvinskia, sect. Osteocaulis, sect. Scopulincola, sect. Spathifolium and sect. Spinosi. Five of these are segregates from sect. Erigeron sensu Cronquist. Sect. Linearifolii, comb. nov., replaces sect. Pycnophyllum Cronq. The justification for maintaining Darwiniothamnus as a distinct genus is weak; it should be returned to Erigeron. Erigeron veracruzensis nom. nov. replaces the later homonym E. scaberrimus (Less.) Nesom.

KEY WORDS: Erigeron, Asteraceae, New World, systematics.

I present a synopsis of the taxonomy and nomenclature of the New World (primarily North American) species groups of Erigeron. In this, I have attempted to list all of the accepted species that occur in North America (including México) and Central America. I have not dealt with South American species included by Solbrig (1962) in sect. Erigeron; I am studying the species of Erigeron (ca 20) in the Antilles. This infrageneric taxonomy certainly will undergo modifications as concepts of relationships within the genus are developed and refined and as other names may be discovered in surveys of older literature. I believe it is important, however, to point out as clearly as possible the great amount of diversity that exists within Erigeron. This is particularly significant as botanists begin comprehensive investigations of the relationships among genera of Astereae. The approach taken here differs strongly from Cronquist's more inclusive view (1947) of sect. Erigeron, which I have partitioned into eight sections. Such hypotheses represent a step toward understanding phylogenetic patterns within this large group of species,

and I believe there is at least heuristic value in presenting them as formal taxonomic proposals.

The "probable relationships" diagram presented by Cronquist (1947, p. 125) and the comments in the text of his revision have been valuable in indicating groups of inter-related species, and his insights remain largely correct. In attempting simply to delimit monophyletic groups, however, I hope to provide a useful and more objective taxonomy. Even then, because of the large degree of suspected morphological parallelism in the genus, hypotheses regarding the constitution of single lineages are speculative to a degree, but those regarding the phyletic derivations between species and lineages are even more so. Molecular approaches may be more incisive than strictly morphological ones in discovering patterns of common ancestry.

In my opinion, among the most important morphological characters for indicating sectional relationships in Erigeron are the behavior of the ligules of the ray flowers (coiling, reflexing, remaining straight, or closing upwards at night) and the behavior of the buds (erect, sharply nodding or archingpendant). These are features of necessity observed in the field, because they often are not preserved in pressed and dried specimens. The plant habit and the nature of leaf insertion are also significant. Clasping leaves are almost completely restricted to the plants of sect. Cincinnactis, sect. Fruticosus, sect. Olygotrichium and sect. Polyactis, although this feature is not strictly diagnostic of any of these groups. Leaf lobing or toothing is characteristic of only six sections. Some species of sect. Wyomingia typically have numerous (4-14) achenial ribs in contrast to the usual number in the genus, two per achene. I believe that achene shape will also prove to be a significant feature in assessing relationships, but I have not emphasized that feature in this study. Basally caducous pappus bristles occur in only one section (sect. Polyactis), where they are diagnostic.

Asa Gray recognized six sections of Erigeron in 1841 but by 1884 had reduced the number to three (sects. Erigeron, Trimorpha and Caenotus), submerging the others into sect. Erigeron. Cronquist included 99 of the 133 of the North American species (in 1947) in a heterogeneous sect. Erigeron. Solbrig (1960, 1962), too, placed most of the South American species of the genus in sect. Erigeron, recognizing only three species in sect. Leptostelma (see below).

In a treatment of the Compositae of the U.S.S.R, Botschantzev (1959) recognized three subgenera: subg. Erigeron (four sections), subg. Trimorpha (two sections), and subg. Conyzastrum (Boiss.) M. Pop. [sect. Conyzastrum and sect. Psychrogeton (Boiss.) Botsch.]. The latter section was recently treated by Grierson & Reichinger (1982) as a separate genus, and I regard Trimorpha as a genus distinct from Erigeron (Nesom 1989b). I attempted to deal with some of Botschantzev's nomenclature here because a few of the

Asian and American species and groups cross the Bering Straits and occur on both continents. *Conyzastrum* and *Psychrogeton* are not included, because all the species appear to be Asian.

Among the first sectional names in Erigeron were those proposed in 1830 by G. Don in Loudon's Hortus Britannicus (see Sundberg & Jones 1987; 1988). Most of Don's groups in Erigeron were highly polyphyletic, and I have tried to lectotypify them in a way that will displace as few new names as possible in Erigeron and related genera. The name of one of Don's sections, however, must supplant a name in current usage, and one of them in Aster, as recently lectotypified with a species of Erigeron by Sundberg & Jones, assumes a position of priority over a name already in use in Erigeron.

Nuttall (1818, 1840) proposed names for several sections of *Erigeron* and I have tried to maintain these with appropriate lectotypes where possible. Such is also true for names proposed by Torrey & Gray (1841).

Rydberg (1906, 1918) introduced numerous infrageneric names as subheadings of his keys to species of Erigeron. In an earlier paper (Nesom 1982), I did not regard these as formal taxonomic proposals because Rydberg gave no indication of the intended rank of these groups and provided neither descriptions nor diagnoses. Further, several species of Erigeron key out in more than one subdivision. Here, however, following Jones (1980) in Aster, I have adopted Holmgren's point of view (1979) in regarding Rydberg's names as validly published, unranked species groups that may be used as basionyms in future combinations. In contrast, Macbride & Payson (1917) accepted one of Rydberg's aggregate names (see sect. Tridactylia below) with the following rationale: "... from the fact that the name was given in the plural form and appears to be just above the rank of species it may well be considered as designating a series" Thus, I have attributed this formal taxon primarily to Macbride & Payson, not as a combination, in exception to Holmgren's view.

Rydberg in 1906 clearly had a view of taxonomy in Erigeron that encompassed more than only the Colorado species, because the names of several species groups (e.g., Acres, Radicati, Decumbentes) were based on epithets of taxa occurring in the Great Plains but not in Colorado. In Rydberg's broader treatment of 1918, each of these three groups included the species upon which its name was based. I have accepted these species as the types of their nomenclaturally corresponding sections, since I believe that clearly was Rydberg's intention.

The following text presents sections of Erigeron, generic segregates, and groups originally in Erigeron but transferred into other genera. Unless specifically stated to the contrary, all infrageneric names cited are in Erigeron. Species marked by an asterisk (*) are ones that occur strictly in México and/or Central America. Names of accepted sections as well as lists of species

are presented alphabetically. Comments on putative relationships are in the text.

I follow Cronquist (1947) and Hultén (1968) in conforming to the use of masculine endings in *Erigeron*, although Linnaeus regarded the genus as neuter. The International Code of Botanical Nomenclature (1988) notes that *Erigeron* is a masculine name "for which botanical usage has re-established the classical gender despite another choice by Linnaeus."

I. SECTIONS OF ERIGERON

Erigeron sect. Arenarioides (Rydb.) Nesom, comb. et stat. nov. Based on Erigeron (sp.-group) Arenarioides Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. arenarioides (D. Eaton ex A. Gray) Rydb.

Additional species in sect. Arenarioides: E. salmonensis Brunsfeld & Nesom, ined. (Brunsfeld & Nesom [in press]).

These two species clearly are closely related between themselves, and I can find no other group whose unity would not be unsettled by their inclusion. Cronquist (1947) has suggested that Erigeron arenarioides may be related to E. oxyphyllus (see comments under sect. Oxyphyllum). Erigeron nematophyllus shares features of habit with these two species, but it has prominently coiling ligules and I include it in sect. Wyomingia.

Sect. Arenarioides is characterized by the following: tap-rooted perennials; caudex branches with densely packed, adherent leaf bases, each branch producing erect, wiry, distally branched stems; leaves ascending-appressed, entire; buds erect; heads turbinate-campanulate; and ray flowers few, with ligules not reflexing or coiling.

- Sect. Asteroidea Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:308. 1841. LEC-TOTYPE (designated here): E. decumbens Nutt. Nuttall also included E. corymbosus Nutt., E. filifolius Nutt., E. foliosus Nutt., E. nanus Nutt., E. ochroleucus Nutt., E. pedatus Nutt. (=E. compositus Pursh) and E. radicatus Hook.
- Erigeron sect. Pseuderigeron Torrey & A. Gray, Fl. N. Amer. 2(1):177.
 1841. LECTOTYPE (designated here): E. caespitosus Nutt. Torrey & Gray also included E. filifolius Nutt., E. douglasii Torrey & A. Gray (=E. foliosus Nutt.), E. decumbens Nutt., E. corymbosus Nutt. and E. ochroleucus Nutt.
- Erigeron sect. Stenactis Torrey & A. Gray, Fl. N. Amer. 2(1):172. 1841. LECTOTYPE (designated here): E. pumilus Nutt. Other species included by Torrey & Gray: E. glaucus Ker Gawler, E. speciosus (Lindley) DC., E. glabellus Nutt., E. concinnus (Hook. & Arn.) Torrey & A. Gray. See discussion in Nesom (in press).

- Asterigeron Rydb., Fl. Rocky Mts. 891. 1918. TYPE: A. watsonii (A. Gray) Rydb. [= Erigeron watsonii (A. Gray) Cronq.].
- Erigeron (sp.-group) Caespitosi Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. caespitosus Nutt.
- Erigeron (sp.-group) Decumbentes Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. decumbens Nutt.
- Erigeron (sp.-group) Pumili Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. pumilus Nutt.
- Erigeron (sp.-group) Radicati Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. radicatus Hook.
- Erigeron (sp.-group) Asperuginei Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. asperugineus (D.C. Eaton) A. Gray.
- Erigeron (sp.-group) Laetevirentes Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. laetevirens Rydb. (=E. ochroleucus Nutt.).
- Erigeron (sp.-group) Filifolii Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. filifolius (Hook.) Nutt.

The plants of sect. Asteroidea are perennials from thick taproots (except in the E. ursinus group) producing mostly scapose, monocephalous stems. Also, the leaves are entire; the buds are erect; the disc corollas are narrowly tubular; the ligules of the ray corollas often dry dark blue and have a tendency (strong in some, weak or not at all evident in others) to coil at the tips, but others appear to reflex (see comments below); and the achenes tend to be narrowly oblong. The plants typically grow in open, level or sloping, sometimes rocky sites at medium elevations, often with sagebrush. Both Torrey & Gray and Nuttall saw the reality of this section, because sect. Pseuderigeron and sect. Asteroidea as originally described each included only a single species that I believe is part of a different lineage. Cronquist's "Group X" of his sect. Erigeron (1947) also included mostly species of sect. Asteroidea.

I have divided sect. Asteroidea into several groups and listed the species accordingly.

1. The E. decumbens group: E. asperugineus (D. Eaton) A. Gray, E. canaani Welsh (=E. eatonii sensu Strother & Ferlatte, 1988), E. decumbens Nutt., E. eatonii A. Gray, E. jonesii Cronq., E. lassenianus E. Greene (incl. E. flexuosus Cronq.), E. nevadincola S.F. Blake, E. sonnei E. Greene, E. wahwahensis Welsh (=E. jonesii sensu Strother & Ferlatte, 1988) and E. watsonii (A. Gray) Cronq.

This group is characterized by simple caudices (multicipital caudices occur but uncommonly), strongly decumbent stem bases that are often purplish, and a thickened node of wood and old petiole bases at the root-stem junction.

The leaves of all species except E. watsonii typically or at least frequently have 3-nerved leaves.

Strother & Ferlatte (1988) revised the taxonomy of this group, which they referred to as "Erigeron eatonii and allied taxa" According to them, all of the taxa of this group "... seem to be very closely related; they variously intergrade morphologically and may constitute a single, polymorphic species." I believe two additional species belong with this species group: Erigeron asperugineous, which previously has been thought to be more closely related to E. clokeyi (Cronquist, 1947; Ake, 1984) and the diminutive E. watsonii, although it is apparently set apart from the rest.

2. The E. ursinus group: E. gracilis Rydb. and E. ursinus D. Eaton.

These two species are a very closely related pair distinct from the other species of sect. Asteroidea in their somewhat diffuse system of rhizomes. In their purple, decumbent stem bases, they appear to be most similar to the E. decumbens group.

3. The E. caespitosus group: E. abajoensis Cronq., E. awapensis Welsh, E. caespitosus Nutt., E. maguirei Cronq., E. nauseosus (M.E. Jones) A. Nels., E. ovinus Cronq., E. subglaber Cronq., E. vetensis Rydb. and E. zothecinus Welsh.

This group is characterized by multicipital caudices and relatively broad, often 3-nerved basal leaves. There is some overlap in morphology with the E. decumbers group. Further, the ray corollas of E. vetensis and E. nauseosus have ligules that appear to reflex, setting these two species apart from the others and perhaps linking them with the E. pumilus group. In placing E. zothecinus here, I follow Welsh (1986) who compared it to E. abajoensis in the diagnosis.

4. The E. corymbosus group: E. corymbosus Nutt., E. filifolius Nutt. and E. ochroleucus Nutt. (incl. E. lackschewitzii Nesom & Weber).

These three species have narrowly lanceolate or oblanceolate leaves and the ligules of the ray flowers are typically long and prominently coiling at the tips. Erigeron filifolius and E. corymbosus typically have branched stems; Erigeron ochroleucus is variable in this respect and in other features.

5. The E. radicatus group: E. disparipilus Cronq., E. latus (A. Nelson & Macbr.) Cronq., E. nanus Nutt., E. parryi Canby & Rose, E. poliospermus A. Gray, E. pygmaeus (A. Gray) E. Greene, E. radicatus Hook. and E. rydbergii Cronq.

The Erigeron radicatus group is characterized by multicipital caudices and strictly erect, relatively short, linear to narrowly oblong or narrowly oblanceolate, 1-nerved, basal leaves.

6. The E. pumilus group: E. aphanactis (A. Gray) E. Greene, E. clokeyi Cronq., E. concinnus (Hook. & Arn.) Torrey & A. Gray, E. engelmannii A. Nels. and E. goodrichii Welsh.

The species of the Erigeron pumilus group are similar in habit and leaf shape to the E. radicatus group or perhaps somewhat intermediate to those of the E. radicatus and E. caespitosus groups. The E. pumilus group tends to be strikingly hispid in appearance, and most significantly, the ligules of the ray corollas appear to reflex. I have not seen E. goodrichii but tentatively include it here on the basis of the discussion by Welsh (1983), who noted that its affinities are with E. clokeyi and E. asperugineous.

Groups 4-6 of sect. Asteroidea are much in need of a comprehensive taxonomic study that includes field observations. The apparent occurrence of two distinctive ligule behaviors suggests that two lineages may be involved and that the groups as I have arranged them may be somewhat artificial.

*Erigeron coronarius E. Greene, *E. janivultus Nesom and three undescribed species perhaps belong here, near the E. pumilus group. I am currently studying this group and defer making a formal judgment on its taxonomic placement until the completion of the study.

Erigeron sect. Cincinnactis Nesom, sect. nov. TYPE: *Erigeron longipes DC.

Folia marginibus dentatis, gemmae plus minusve erectae, corollae radii numerosae in 1-3 seriebus cincinnatae ad maturitatem plerumque perangustae, achenia brevi-oblongae parvulae costis manifeste aurantiacis, pappus plerumque sine serie externa.

Additional species in sect. Cincinnactis: *E. basilobatus S.F. Blake, *E. crenatus Eastw., *E. exilis A. Gray, *E. narcissus Nesom, *E. oaxacanus Greenman, E. procumbens (Houston ex P. Miller) Nesom (=E. myrionactis Small), *E. socorrensis I.M. Johnston, *E. tephropodus Nesom, *E. veracruzensis Nesom and *E. stanfordii I.M. Johnston ex Nesom.

The peculiar habit of Erigeron exilis is similar to that of species of sect. Linearifolii, but the behavior of its ligules allies it with sect. Cincinnactis.

In an earlier publication (Nesom & Sundberg 1985), I included Erigeron longipes as a synonym of Erigeron scaberrimus (Less.) Nesom. The two, however, are distinct species. Further, the name E. scaberrimus had already been proposed for a South American species, making my combination a later homonym. A new name is provided here for the Mexican species, which occurs from Tamaulipas, Veracruz, Puebla and Oaxaca.

Erigeron veracruzensis Nesom, nom. nov. Based on Aster scaberrimus Less., Linnaca 5:143. 1830. E. scaberrimus (Less.) Nesom, 1985; non E. scaberrimus Gardner, 1848.

A group of primarily Caribbean species with tightly coiling ligules apparently also belongs in *Erigeron* sect. *Cincinnactis*. Two of them, *E. bellioides* DC. and *E. cuneifolius* DC., occur in México, where they probably are adventive.

The plants of sect. Cincinnactis are characterized by the following: leaves with toothed margins, buds nodding; rays usually filiform and numerous (up to 300) in 1-3 series, tightly coiling at maturity, or only at the tips in species with longer ligules, usually very narrow; achenes short-oblong and very small, with prominent orange ribs; pappus usually without an outer series. All but one species (E. narcissus) are perennials from short, fibrous-rooted rhizomes. All are from México and Central America although E. procumbens ranges northward into the southeastern United States.

Sect. Erigeron L., Sp. Pl. 863. 1753. LECTOTYPE (see discussion below): E. uniflorus L.

Linnaeus included the following species in Erigeron:

- E. uniflorus L.
- E. acris L.
- E. alpinus L.
- $E.\ philadelphicus\ L.$
- E. carolinianus L. (see Fernald 1944, and comments below, following "GENUS UNKNOWN."
- E. canadensis L. [=Conyza canadensis (L.) Cronq.]
- E. bonariensis L. [= Conyza bonariensis (L.) Cronq.]
- E. gramineus L. [=Arctogeron gramineus (L.) DC.]
- E. siculus L. [=Pulicaria sicula (L.) Moris]
- E. camphoratus L. [=Pluchea camphorata (L.) DC.]
- E. tuberosus L. [=Jasonia tuberosa (L.) DC.]
- E. viscosus L. [=Inula viscosa (L.) Aiton]
- Erigeron sect. Uniflori G. Don in Loudon, Hort. Brit. 343. 1830. TYPE: E. uniflorus L. Don also listed E. alpinus L., E. compositus Pursh and E. gramineus L. [=Arctogeron gramineus (L.) DC.].
- Aster sect. Pauciflori G. Don in Loudon, Hort. Brit. 346. 1830. LEC-TOTYPE (Sundberg & Jones 1987): A. pulchellus Willd. (=Erigeron venustus Botsch.).

- Erigeron (sp.-group) Uniflori Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. uniflorus L.
- Erigeron sect. Monocephali Vierh., Beih. Bot. Centralbl. 19:492. 1906. LECTOTYPE (designated here): E. uniflorus L.
- Erigeron sect. Siphonoglossa Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 16:393. 1954. TYPE: E. uniflorus L.
- Erigeron sect. Platyglossa Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 16:388. 1954. TYPE: Erigeron venustus Botsch.

Sect. Platyglossa is tentatively included as a synonym of sect. Erigeron although Botschantzev included in it several species that are members of sect. Fruticosus [e.g., E. peregrinus (Banks ex Pursh) E. Greene, E. thunbergii A. Gray]. Erigeron venustus does not appear to be closely related to these species (Nesom 1982) but rather to be more similar to those of sect. Erigeron.

Additional North American species of sect. Erigeron: E. algidus Jepson (=E. petiolaris E. Greene, non Vierh.), E. alpiniformis Cronq., E. arthurii B. Boivin, E. aureus E. Greene, E. eriocephalus Vahl, E. evermannii Rydb., E. flettii G.N. Jones, E. grandiflorus Hook., E. humilis Graham, E. hultenii Spongberg, E. hyperboreus E. Greene, E. lanatus Hook., E. melanocephalus A. Nelson, E. mexiae K. Becker, E. muirii A. Gray, E. simplex E. Greene, E. yukonensis Rydb.

This view of sect. Erigeron restricts it essentially to monocephalous plants of alpine and subalpine habitats, at least in North America. In addition, these plants are perennials from short, fibrous-rooted rhizomes and have entire leaves, erect buds and coiling ligules. Spongberg (1969), who included most of these species in a biosystematic study, found evidence for reticulate interrelationships among a number of them. He observed that "in North America, few species at lower altitudes in the Cordillera appear to be truly implicated with arctic-alpine species of Erigeron" and that their nearest relatives are "likely to be found in the mountains of Central Asia and the Caucasus."

Species with a monocephalous habit are found in every section of Erigeron except sect. Arenarioides (two species), sect. Oxyphyllum (two species) and sect. Phalacroloma (two species, perhaps belonging with sect. Olygotrichium). In sects. Fruticosus, Karvinskia, Leptostelma, Olygotrichium and Polyactis, it seems relatively clear that branched capitulescences are primitive, but in the other groups, including sect. Erigeron, it seems likely that monocephaly is primitive and that a branching habit has been derived from ancestors with simple, monocephalous stems.

In searching for an area of common ancestry between Erigeron and Aster, Cronquist (1947) emphasized the branching, leafy, Aster-like habit of species of Erigeron sect. Fruticosus. There are boreal, monocephalous species of Aster, however, that also appear to straddle a different, somewhat arbitrary

morphological boundary between Aster and Erigeron, e.g., A. alpinus L. and A. alpigenus (Torrey & A. Gray) A. Gray.

Two lectotypes have been selected for Erigeron by previous botanists.

- E. acris L. [Britton N.L. & A. Brown, Illus. Fl. N. U.S. (ed. 2) 3:436. 1913].
- E. uniflorus L. (Green, M.L., Prop. Brit. Bot. 181. 1929).

I accept Erigeron uniflorus as the lectotype and reject the earlier choice for several reasons. Most significantly, the choice of E. acris as the type of Trimorpha and later of Erigeron sect. Trimorpha were made before its selection by Britton & Brown as the lectotype of Erigeron (sect. Erigeron). Further, the relatively few (ca 40-45) species of sect. Trimorpha are very distinct in their trimorphic florets from the remainder of the genus. Trimorpha has been treated as a genus (Vierhapper 1906) and as a subgenus (Botschantzev 1959), and I have resegregated it as a genus (Nesom 1989b). In this case, if E. acris were the type of Erigeron, more than 300 species would have to be renamed in a genus now understood to be one of the various synonyms of Erigeron. Finally, the choice of the generic name ("early old age") by Linnaeus probably was intended to reflect the appearance of the densely woolly-villous involucres of some of the species. Erigeron uniflorus shows this feature, E. acris does not.

Cronquist (pers. comm.) has added his agreement with this choice of a lectotype with the following comment: "Pennell pointed out to me many years ago that Linnaeus often based his descriptions for Genera Plantarum on a single species, which if it can be identified becomes the logical lectotype. Linnaeus' description in Genera Plantarum is scarcely compatible with E. acris, although it would fit E. uniflorus and some other species."

- Sect. Fruticosus G. Don in Loudon, Hort. Brit. 343. 1830. TYPE: "E. glaucus B.R." (=E. glaucus Ker Gawler, Bot. Reg., 1815). Monotypic as recognized by Don.
- Erigeron sect. Pauciflori G. Don in Loudon, Hort. Brit. 343. 1830. LEC-TOTYPE (designated here): E. bellidifolius Willd. (=E. pulchellus Michx.). Don also included Erigeron caucasicas Stev., E. nudicaulis Michx. (=E.vernus (L.) Torrey & A. Gray), E. glabellus Nutt., E. jamaicensis L. and E. montevidensis Spreng. [according to Solbrig (1962), this plant probably represents a species of Conyza].
- Musteron Rafin., Fl. Tellur. 2:50. 1836. TYPE: "M. bellidifolium" Rafin. Probably =E. bellidifolius Willd. (=E. pulchellus Michx.). Monotypic as recognized by Rafinesque.
- Fragmosa Rafin., Fl. Tellur. 2:50. 1836. LECTOTYPE (designated here): E. nudicaulis Michx. [=E. vernus (L.) Torrey & Gray]. Also included in Fragmosa by Rafinesque were E. uniflorus L., E. alpinus L., E. pumilus Nutt., E. asper Nutt. (=E. glabellus Nutt.) and E. glabellus Nutt.

- Woodvillea DC., Prodr. 5:318. 1836. TYPE: W. calendulacea DC. (=E. glaucus Ker Gawler). Monotypic as recognized by de Candolle.
- Erigeron sect. Phoenactis Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:310. 1840. LECTOTYPE (designated here): E. speciosus (Lindl.) DC. Other species included by Nuttall: E. macranthus, E. hispidum Nutt. (=E. glaucus Ker Gawler), E. maritimum Nutt. (=E. glaucus Ker Gawler).
- Erigeron sect. Erigeridium Torrey & A. Gray, Fl. N. Amer. 2(1):176. 1841. TYPE: E. vernus (L.) Torrey & A. Gray. Monotypic as recognized by Torrey & Gray (see comments below).
- Erigeron (sp.-group) Elatiores Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. elatior (A. Gray) E. Greene.
- Erigeron (sp.-group) Salsuginosi Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. salsuginosus (Rich.) A. Gray [=E. peregrinus subsp. callianthemus (E. Greene) Cronq.]. See Cronquist (1947), however, for comments on the misapplication of the name Aster salsuginosus Rich.
- Erigeron (sp.-group) Macranthi Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. macranthus Nutt. [=E. speciosus (Lindl.) DC.].
- Erigeron (sp.-group) Glabelli Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. glabellus Nutt.
- Erigeron (sp.-group) Asperi Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. asper Nutt. (=E. glabellus Nutt.).
- Erigeron (sp.-group) Verni Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: E. vernus (L.) Torrey & A. Gray
- Erigeron (sp.-group) Pulchelli Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: E. pulchellus Michx.
- Erigeron sect. Peregrinus Nesom, Syst. Bot. 7:463. 1982. TYPE: E. peregrinus (Banks ex Pursh) E. Greene. In an earlier paper (Nesom 1982), I included 34 species in this section but now believe that eight (those lacking a pappus of bristles) should be segregated as a distinct group (see sect. Imbarba below).

Species of sect. Fruticosus: E. aliceae J. Howell, E. arizonicus A. Gray, E. cascadensis A. Heller, E. cervinus E. Greene, E. coulteri Porter, E. elatior (A. Gray) E. Greene, E. eximius E. Greene, E. formosissimus E. Greene, E. garrettii A. Nelson, E. glabellus Nutt., E. glaucus Ker Gawler, E. hessii Nesom, E. howellii A. Gray, E. kuschei Eastw., E. leibergii Piper, E. oreganus A. Gray, E. peregrinus (Pursh) E. Greene, E. platyphyllus E. Greene, *E. potosinus Standley, E. pulchellus Michx., E. rusbyi A. Gray, E. rybius Nesom, E. sanctarum S. Watson, E. speciosus (Lindley) DC., E. subtrinervis Rydb.,

E. supplex A. Gray, E. thunbergii A. Gray "complex," E. uintahensis Cronq. and the E. palmeri group (see below).

Sect. Fruticosus is characterized by the following: perennials mostly from short, thick, fibrous-rooted rhizomes; leaves often 3-nerved, entire or less commonly slightly toothed, the cauline more or less equably distributed, little reduced from the basal, usually at least the upper or lower clasping; buds erect or on slightly curved peduncles; phyllaries in 2-4 equal or nearly equal series, herbaceous, narrowly lanceolate with attenuate, often flexuous tips; ray corollas usually long and coiling at the tips. See Nesom (1982) for comments on problems in circumscribing this group and a discussion on a putative relationship between sect. Erigeron and sect. Fruticosus.

The E. palmeri group.

Four pappose species restricted to México, closely inter-related among themselves, appear to be members of sect. Fruticosus: *E. hintoniorum Nesom, *E. morelensis Greenm., *E. palmeri A. Gray and *E. wellsii Nesom.

Erigeron vernus (L.) Torrey & A. Gray of the southeastern United States, also belongs to the E. palmeri group. This species was the basis for the monotypic sect. Erigeridium of Torrey & Gray, but Cronquist (1947) included it as a member of sect. Olygotrichium. It has smaller heads on more branched stems than its closest relatives, but the thick, dull green and nearly glabrous basal leaves with remotely and shallowly toothed margins are nearly identical to those of E. palmeri. Further, both species have thick, fibrous roots with no rhizome. The long disc style appendages of E. vernus, the erect buds and the rays not closing upwards at night are also distinctive.

The position of Erigeron pulchellus.

The only species of sect. Fruticosus besides Erigeron vernus in the eastern United States is E. pulchellus. Earlier (Nesom 1982), I was equivocal about its taxonomic placement. It is similar to E. philadelphicus (sect. Olygotrichium) in aspects of its capitular morphology and its numerous, thinherbaceous, clasping, cauline leaves. Clasping leaves, however, are also typical of sect. Fruticosus, and I believe Cronquist (1947) was correct in noting the distinctness of the scale-leaved, stoloniform rhizomes of E. pulchellus. Similar rhizomes are not produced in sect. Olygotrichium, but they are found in several species of sect. Fruticosus (e.g., E. rybius, E. eximius, E. potosinus). Further, E. pulchellus has erect buds and large heads with rays that do not close upwards at night, and the ligules of some collections can be seen to be distinctly coiling, all traits typical of sect. Fruticosus but found in no species of sect. Olygotrichium.

Erigeron sect. Imbarba Nesom, sect. nov. TYPE: *Erigeron galeottii (A. Gray ex Hemsley) E. Greene.

Gemmae erectae, phyllaria 2-porcata ad basim, corollae radii cincinnatae ad maturitatem, setae pappo carentes vel paucae dispersim praesentes.

Additional species in sect. Imbarba: *E. astranthioides De Jong & Nesom, *E. forreri (E. Greene) E. Greene, *E. fraternus E. Greene, *E. guatemalensis (S.F. Blake) Nesom, *E. mimus (S.F. Blake) Nesom and *E. strigulosus E. Greene.

I first included these eight species (Nesom 1982) as members of sect. Peregrinus (=sect. Fruticosus) but now believe there is as much evidence to suggest they represent a sister taxon of the latter as a derivative group of it (Nesom in prep.). These species are distinguished by their toothed leaves, erect buds, basally 2-ridged phyllaries, distally coiling ligules of the ray flowers and essential lack of pappus bristles. Except for E. strigulosus, a taprooted annual, they are all perennials from short, fibrous-rooted rhizomes. All occur in México and Guatemala.

Erigeron sect. Karvinskia Nesom, sect. nov. TYPE: *E. karvinskianus DC.

Plantae perennia, folia basalia decidua ab florescentia, folia caulinae obovatae dentatae plus minusve pariter distributae, gemmae erectae, corollae radii nec cincinnatae nec reflexae non clausae sursus nocte.

Additional species of sect. Karvinskia: *E. heteromorphus B. Robinson, *E. irazuensis Greenman and *E. pacayensis Greenman.

Plants of this section are characterized by the following features: perennials from thin, woody taproots or short rhizomes, leaves mostly obovate, toothed, all cauline by flowering and distributed more or less equably on the stems, buds erect, ligules of the ray flowers neither coiling nor reflexing and not closing upwards at night. In addition to those listed above, there are two additional but undescribed species of sect. Karvinskia from México and Central America. The group is presently under study by me. Sect. Karvinskia may prove to be closely related to sect. Linearifolii, but the broader, toothed leaves and equal phyllaries of the former and the habit of the latter are distinctive.

Erigeron sect. Linearifolii (G. Don) Nesom, comb. nov. Based on Aster sect. Linearifolii G. Don in Loudon, Hort. Bot. 346. 1830. LECTO-TYPE (Sundberg & Jones 1987): A. graminifolius Pursh (=E. hyssopifolius Michx.).

Erigeron sect. Pycnophyllum Cronq., Brittonia 6:141. 1947. TYPE: E. foliosus Nutt.

Sundberg & Jones (1987) lectotypified Don's sectional epithet to preserve an established one in *Aster*; by doing so, however, they moved Don's name into a position of priority over Cronquist's sect. *Pycnophyllum*.

Species of sect. Linearifolii: E. aequifolius H.M. Hall, E. breweri A. Gray, *E. chiangii Nesom, E. foliosus Nutt., E. hyssopifolius Michx., E. inornatus A. Gray, *E. lepidopodus (B. Robinson & Fern.) Nesom, E. miser A. Gray, E. petrophilus E. Greene, E. rhizomatus Cronq. and *E. scoparioides Nesom.

In earlier publications, I did not clearly recognize the relationships of the three Mexican species of this section. Erigeron lepidopodus from Chihuahua and northern Durango, México, however, is clearly the sister species of Erigeron rhizomatus, endemic to Catron and McKinley counties, New Mexico. Erigeron chiangii and E. scoparioides, species of northeastern México, are probably sister taxa.

The species of sect. Linearifolii are characterized by the presence of numerous, linear or narrowly oblong, entire leaves, borne on short internodes and essentially uniform from base to near top of the plant. They are perennial, often with long, slender, caudex-like, lower branches. The buds are erect, the phyllaries are usually strongly graduated (though not in the type species) and the rays have ligules straight or slightly coiling at the tips.

- Sect. Olygotrichium Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:311. 1840. LECTOTYPE (designated here): E. divaricatum Nutt. (=E. divergens Torrey & A. Gray). Nuttall also included E. tenuis Torrey & Gray, E. strigosus Muhl. ex Willd. and E. "occidentalis" (?=E. strigosus Muhl. ex Willd.).
- Heterochaeta DC., Prodr. 5:282. 1836; non Besser ex Schultes & Schultes, 1827. LECTOTYPE (designated here): Erigeron pubescens Kunth. De Candolle also included E. gnaphalioides Kunth (=Conyza confusa Cronq.) and four extra-American species.
- Erigeron (sp.-group) Philadelphici Rydb., Fl. Colorado 359. 1906, in clave; non Small, 1933. TYPE: E. philadelphicus L.
- Erigeron (sp.-group) Bellidiastra Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. bellidiastrum Nutt.
- Erigeron (sp.-group) Divergentes Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. divergens Torrey & A. Gray.
- Erigeron (sp.-group) Flagellares Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. flagellaris A. Gray

Species of sect. Olygotrichium: E. bellidiastrum Nutt., *E. bigelovii A. Gray, *E. calcicola Greenman, E. colomexicanus A. Nelson, E. divergens Torrey & A. Gray (incl. E. solisaltator Nesom), *E. dryophyllus A. Gray, E. flagellaris A. Gray, *E. fundus Nesom, E. geiseri Shinners, E. gilensis

Woot. & Standl., *E. gypsoverus Nesom, E. lemmonii A. Gray, E. lobatus A. Nelson, *E. metrius S.F. Blake, *E. mihianus S.F. Blake, E. mimegletes Shinners, E. modestus A. Gray, E. multiceps E. Greene, *E. onofrensis Nesom, E. philadelphicus L., *E. pinkavii B. Turner, E. proselyticus Nesom, *E. pubescens Kunth, E. quercifolius Lam., E. religiosus Cronq., E. sionis Cronq., E. tenellus DC., E. tenuis Torrey & A. Gray, *E. turnerorum Nesom, *E. unguiphyllus Nesom, *E. velutipes Hook. & Arn. and *E. versicolor (Greenman) Nesom.

Erigeron sect. Olygotrichium is a relatively large but well defined section. The species are primarily from the southwestern United States and México, with a small group from the eastern United States and the Antilles. They are mostly taprooted annuals or biennials, and though perennials are also included, no other section of Erigeron has so many species of plants of annual-biennial duration. They have prominently lobed or toothed leaves, nodding buds, small heads and narrow ligules often with a lilac midstripe on the lower surface. The ligules close upwards at night, neither reflexing nor coiling with maturity. This ligule behavior apparently is unique among the sections of Erigeron, but it is known from other genera of Astereae (e.g., Aphanostephus and at least some species of Townsendia). Four species, E. mimegletes, E. versicolor, E. gilensis and an undescribed species from Chihuahua, are epappose.

A group of inter-related species from the Antilles also appears to belong in sect. Olygotrichium: E. caeruleus Urban, E. dissectus Urban, E. jamaicensis L. and E. pinetorum Urban. Erigeron psilocaulis Urban differs from these in its non-clasping leaves but probably is part of the same lineage, as is the suffrutescent E. darrellianus Hemsley.

Relationships among the species of sect. Olygotrichium of the eastern and south-central United States are complex. Erigeron philadelphicus, E. quercifolius and E. caeruleus (and its relatives) appear to be closely related. Erigeron tenuis, E. tenellus, E. geiseri and E. turnerorum (northern México) form a closely knit group. Erigeron tenuis, in turn, is very similar to E. strigosus of sect. Phalacroloma. Further comments on the possible relationship between sect. Olygotrichium and sect. Phalacroloma are found under the latter.

As pointed out by Cronquist (1947), Erigeron glabellus (sect. Fruticosus) is in some ways (particularly its short-lived duration and numerous ray flowers with narrow ligules) similar to species of sect. Olygotrichium, and this species may indicate a possible direction of common ancestry for the two sections.

In Cronquist's view, sect. Olygotrichium comprised 20 species. One of these, E. calvus Coville, I consider to be a synonym of E. divergens and another, E. plateauensis Cronq., a synonym of E. modestus. Although Cron-

quist placed E. multiceps E. Greene in sect. Erigeron because of its perennial duration, it is, as he noted, most closely related to E. divergens and belongs in sect. Olygotrichium. Several species cited by Cronquist as members of sect. Olygotrichium are better placed in different groups: E. myrionactis Small (=E. procumbens, sect. Cincinnactis), E. neomexicanus A. Gray and E. oreophilus Greenman, both of which were included by Cronquist in E. delphinifolius (sect. Polyactis), E. glabellus (sect. Fruticosus), E. vernus (sect. Fruticosus) and E. pulchellus (sect. Fruticosus). Comments on the last three species are found under sect. Fruticosus.

Erigeron sect. Osteocaulis Nesom, sect. nov. TYPE: E. linearis (Hook.)
Piper

Bases caulium et foliorum plerumque albido-induratae osseae, gemmae erectae, folia lineares vel oblanceolatae, corollae radii luteae vel caeruleae nec cincinnatae nec reflexae non clausae sursus nocte in specie una abscentes differt.

Erigeron (sp.-group) Lutei Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. luteus A. Nelson [=E. linearis (Hook.) Piper].

Additional species in section Osteocaulis: E. barbellatus E. Greene (rays blue/white), E. bloomeri A. Gray (rayless), E. chrysopsidis A. Gray, E. elegantulus E. Greene (blue/pink rayed) and E. piperianus Cronq.

Sect. Osteocaulis is a well defined natural group whose essential composition was recognized by Cronquist in 1947. It is characterized by the following: perennials from caudices with several, short, erect branches; bases of stems and petioles usually whitish-indurated, bony-textured; buds erect; leaves entire, linear, varying to narrowly oblanceolate in E. barbellatus, stiffly erect; ligules of ray corollas not reflexing or coiling, yellow in three species, bluish in three, one species rayless. The only other yellow-rayed species of Erigeron in North America is E. aureus, which is a member of sect. Erigeron.

Several species of Erigeron sect. Asteroidea also have whitish petiole bases (e.g., E. nanus, E. rydbergii) but the margins are ciliate and the cellular texture is different from that in sect. Osteocaulis.

Cronquist (1947) did not make any comment regarding the putative relationships of Erigeron filifolius, but he did include it as a side branch among the species of sect. Osteocaulis in his "probable relationships" diagram. Erigeron filifolius, however, lacks both the yellow rays and strikingly indurated stem/petiole bases of the taxa that make section Osteocaulis unusual, and I have placed it in sect. Asteroidea.

Sect. Phalacroloma (Cass. in Cuvier) Torrey & A. Gray, Fl. N. Amer. 2(1):175. 1841. Based on Phalacroloma Cass. in Cuvier, Dict. Sci. Nat. 39:404. 1826. TYPE: P. obtusifolia Cass. (=E. strigosus Muhl.

- ex Willd.). Cassini also included P. acutifolia Cass. [=E. annuus (L.) Pers.] in the genus.
- Diplemium Rafin., Fl. Tellur. 2:50. 1836. LECTOTYPE (designated here): Erigeron strigosus Muhl. ex Willd. Rafinesque also included Erigeron nervosus Willd. [=Heterotheca graminifolia (Michx.) Elliott], Erigeron quercifolius Lam. and Erigeron carolinianus L.
- Erigeron (sp.-group) Ramosi Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. ramosus (Walter) B.S.P. (=E. strigosus).
- Erigeron (sp.-group) Annui Small, Man. Southeastern Fl. 1395. 1933, in clave. TYPE: E. annuus (L.) Pers.

Cassini was not sure whether Phalacroloma obtusifolia might be the same species as Erigeron hyssopifolius Michx. or E. carolinianus L. "This confusion commenced with Pursh, who erroneously adduced the figure of Dillenius and the E. Carolinianus as synonyms of the E. hyssopifolium of Michaux" (Gray 1841). This putative synonymy was repeated by Cassini, de Candolle and Lessing. Cassini's description of the pappus and discussion of the characters of Phalacroloma leave little doubt, however, as Gray (1841) early realized, that the type was E. strigosus (see Fernald 1944, for further comments on the identity of Erigeron carolinianus).

Torrey & Gray (1841) included as members of sect. Phalacroloma: E. strigosus, E. annuus, E. tenuis and E. divergens, the last two of sect. Olygotrichium. Cronquist (1947) included only the two species lacking pappus bristles on the ray achenes, Erigeron strigosus and E. annuus, but, as he noted, E. tenuis is very similar to E. strigosus and sect. Phalacroloma may be only artificially separated from sect. Olygotrichium. Both species of sect. Phalacroloma are annuals with slightly to prominently nodding buds. The leaves of E. annuus are strongly toothed; those of E. strigosus vary from entire to toothed.

Chromosome counts of *Erigeron annuus* have all been triploid; diploid and various polyploid populations of *E. strigosus* have been reported. I speculate that *E. annuus* may be of hybrid origin between *E. strigosus* and some other species of the eastern United States, *E. philadelphicus* being the most conspicuous candidate.

- Sect. Polyactis (Less.) Nesom, Phytologia 66:416. 1989. Based on Polyactis Less., Syn. gen. Comp. 188. 1832. TYPE: Erigeron delphinifolius Willd. Polyactidium DC., Prodr. 5:281. 1836.
- Stenactis Cass. in Cuvier, Dict. Sci. Nat. 37:485. 1825. TYPE: Erigeron delphinifolius Willd. Non Stenactis sensu Nees, 1832; non sensu Less., 1832; non E. sect. Stenactis Torrey & A. Gray, 1841.
- Achaetogeron A. Gray, Mem. Amer. Acad. Arts, n. ser. 4 (Pl. Fendl.):72.

1849. TYPE: Achaetogeron wislizeni A. Gray [=Erigeron wislizeni (A. Gray) E. Greene].

Species of sect. Polyactis: *E. annuactis Nesom, *E. basaseachensis Nesom, *E. caulinifolius Nesom, *E. circulis Nesom, *E. coroniglandifer Nesom, *E. dactyloides (Greenm.) Nesom, *E. delphinifolius Willd., *E. eruptens Nesom, *E. griseus (Greenm.) Nesom, *E. inoptatus A. Gray, *E. nacoriensis Nesom, E. neomexicanus A. Gray, E. oreophilus Greenman, *E. podophyllus Nesom, *E. polycephalus (Larsen) Nesom, *E. rhizomactis Nesom, *E. seemannii (Schultz-Bip.) E. Greene, *E. subacaulis (McVaugh) Nesom and *E. wislizeni (A. Gray) E. Greene.

These species are characterized for the most part by pinnatifid or coarsely toothed leaves, arching-pendant buds, ligules that sharply reflex at the tube-ligule junction and a pappus of bristles that are basally caducous or completely lacking. All occur in western and south-central México; two of them, E. oreophilus and E. neomexicanus, also are found in the southwestern United States. See Nesom (1989a) for details and a discussion of typification of the generic synonyms noted here.

Erigeron sect. Scopulincola Nesom, sect. nov. TYPE: E. scopulinus Nesom & Roth

Plantae parvulae rhizomatosae scopuli habitantes, folia oblanceolatispathulata, corollae radii reflexae.

Additional species in sect. Scopulincola: E. kachinensis Welsh & Moore, E. leiomerus A. Gray and E. pringlei A. Gray.

These species from the southwestern United States appear to form a well defined natural group. The habitat of each is in cracks and crevices of rock faces and cliffs. All are rhizomatous perennials with entire, oblanceolate-spatulate leaves, erect buds and ray flowers with prominently reflexing ligules. In their leaves and habit, these plants are similar to those of sect. Spathifolium, but the peculiar habitat, distinctive rhizomes (vs caudex branches) and reflexing ligules set them apart.

Erigeron sect. Spathifolium Nesom, sect. nov. TYPE: E. tener (A. Gray)
A. Gray

Plantae parvae monocephalae ramis brevibus caudicis, indumentum strigillosum trichomatum alborum arcte adpressorum brevium rigidorum acutorum, folia oblanceolati-spathulatae, gemmae erectae, et corollae radii nec cincinnatae nec reflexae non clausae sursus nocte.

Additional species in sect. Spathifolium: E. acomanus Spellenberg & Knight ined, E. cavernensis Welsh & Atwood, E. cronquistii Maguire, E. tener (A. Gray) A. Gray, E. tweedyi Canby and E. uncialis S.F. Blake.

Nesom:

These six species comprise a relatively well defined natural group of mostly small perennials with long or short caudex branches, ultimately from a taproot, entire, oblanceolate-spatulate leaves, a strigillose indument of closely appressed, white, short, stiff and sharp-pointed hairs; erect buds and ligules that neither coil nor reflex. The stem pubescence of E. uncialis is longer and spreading but otherwise similar. The stems of these plants are simple and monocephalous, except for those of E. tweedyi, which usually are few branched.

Earlier, Nesom & Roth (1981) tentatively placed Erigeron cronquistii closer to sect. Scopulincola. Ake (1984), however, as well as Maguire (1944) in its original description, correctly recognized the relationship of E. cronquistii with E. tener. Atwood & Welsh (1988) noted in their discussion that E. cavernensis is "evidently allied to E. simplex," but they correctly contrasted it with E. uncialis, to which it is most similar, in the diagnosis.

The habit and peculiar pubescence of plants of sect. Spathifolium are similar to those in sect. Wyomingia, and there is a possibility of a close relationship between the two groups.

Erigeron sect. Spinosi (Alexander in Small) Nesom & Sundberg, comb. nov. Based on Aster (sp.-group) Spinosi Alexander in Small, Man. Southeastern Fl. 1365. 1933, in clave. Aster sect. Spinosi (Small) A.G. Jones, Brittonia 32:233. 1980. TYPE: Aster spinosus Benth. (=Erigeron ortegae S.F. Blake)

Additional species in sect. Spinosi: E. oxyphyllus E. Greene.

Sundberg (1986) concluded that A. spinosus is better placed in Erigeron than Aster, but he did not discover that it has such a close relative already placed in Erigeron. The similarity, however, between E. oxyphyllus and A. spinosus is striking. Plants of both produce stems that are 5-25 dm tall, strictly erect, green but somewhat ligneous, glabrous and striate. Further, both are perennial and usually produce many simple stems from a woody, rhizomatous base. The entire leaves are produced early in the season and are quickly deciduous, usually leaving only the green stems by flowering. In both species, the buds are erect, the phyllaries strongly graduated in 4-5 series and the heads solitary or in loose corymbs. On the other hand, the achenes of E. oxyphyllus are strigose and have 2-4 thick, orange, resin-filled ribs, while those of A. spinosus are glabrous, have 5, thinner, light-colored nerves and are not so strongly compressed. The phyllaries with three, orange-resinous veins emphasized by Sundberg as characteristic of A. spinosus are apparent on some plants of E. oxyphyllus (e.g., Peebles & Harrison 5270 [LL]) but not on others. Plants of E. oxyphyllus are not spiny, but neither are some forms of A. spinosus.

Cronquist (1947) described Erigeron oxyphyllus as a "peculiar and wellmarked species ... taxonomically somewhat isolated" but probably related to E. arenarioides. Plants of the latter have erect buds and strongly graduated phyllaries, but in habit they are much smaller with thinner stems and have persistent basal and cauline leaves, and I have placed them in a different section.

The nomenclature and infraspecific taxonomy of Aster spinosus will be treated by Sundberg (in prep.).

The addition of a third species, which is from México and yet undescribed, will somewhat alter the circumscription of sect. *Spinosi*. This will be discussed in the formal proposal of the species (Sundberg & Nesom [in prep.]).

Besides Aster spinosus, Jones (1980) also included A. intricatus (A. Gray) Benth. (=Leucosyris E. Greene) in her Aster sect. Spinosi. See Nesom et al. (in press) for additional comments on the latter species, which is not part of the same group as A. spinosus.

Sect. Tridactylia Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:310. 1841. TYPE: E. compositus Pursh. Monotypic as recognized by Nuttall.

Erigeron series Multifidi Rydb. ex Macbride & Payson, Contr. Gray Herb. 49:73. 1917. Based on Erigeron (sp.-group) Multifidi Rydb., Fl. Colorado 359. 1906, in clave. LECTOTYPE (designated here): E. compositus Pursh. Erigeron (sp.-group) Compositi Rydb., Fl. Rocky Mts. 896. 1918, in clave (Rydberg changed the name of this group in 1918). Macbride & Payson also included E. pinnatisectus (A. Gray) A. Nelson.

Additional species in sect. Tridactylia: E. allocotus S.F. Blake, E. basalticus Hoover, E. flabellifolius Rydb., E. mancus Rydb., E. pallens Cronq., E. pinnatisectus (A. Gray) A. Nelson, E. purpuratus E. Greene, E. salishii Douglas & Packer, E. trifidus Hook. and E. vagus Payson. Becker (1976) described E. meziae Becker, which sometimes has apically tridentate leaves, as a "connecting link" between sect. Erigeron and sect. Tridactylia and it may be a member of the latter.

Most of the species of sect. Tridactylia have pinnatifid leaves; in several, the leaves are apically trilobed. In all species the leaves are non clasping, the buds are erect and the ligules neither coil nor reflex. Also, they are perennials with a strong tendency to produce rhizome like caudex branches.

- Sect. Wyomingia (A. Nelson) Cronq., Brittonia 6:140. 1947. Based on Wyomingia A. Nelson, Bull. Torrey Bot. Club 26:249. 1899. TYPE:
 E. pulcherrimus Heller [= Wyomingia pulcherrima (Heller) A. Nelson].
- Erigeron (sp.-group) Cani Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. canus A. Gray
- Erigeron (sp.-group) Tetrapleuri Rydb., Fl. Rocky Mts. 897. 1918, in clave. TYPE: E. tetrapleuris (A. Gray) Heller (=E. utahensis A. Gray).

The species of sect. Wyomingia are taprooted perennials, and they have entire, more or less linear leaves, a strigillose vestiture of very short and closely appressed hairs, erect buds and prominently coiling ligules. I recognize two groups within the section and list the species accordingly.

1. The E. pulcherrimus group: E. argentatus A. Gray, E. canus A. Gray, E. parishii A. Gray, E. pulcherrimus and E. utahensis A. Gray.

These species have multi-nerved [(2-)4-10(-14)] achenes, a feature restricted mostly to this group. The achenes of *Erigeron* sect. *Spinosi*, however, also may have 4 to 5 ribs, as may those of *E. peregrinus* (sect. *Fruticosus*) and *E. lepidopodus* and *E. rhizomatus* (sect. *Linearifolii*).

2. The E. compactus group: E. carringtonae Welsh, E. compactus S.F. Blake, E. consimilis Cronq., E. nematophyllus Rydb. and E. untermannii Welsh & Goodrich.

Erigeron compactus, E. consimilis and E. nematophyllus were noted by Cronquist (1947) to be "apparently not far removed from the line of descent of the section Wyomingia." They lack the multinerved achenes characteristic of the E. pulcherrimus group and tend to be smaller in stature but are otherwise very similar. Some plants of E. pulcherrimus, however, are small and nearly identical in habit to those of E. compactus. Erigeron nematophyllus is obviously more similar to E. utahensis in its habit of relatively tall, branching stems, which suggests that the taxonomic use of achenial nerves may result in an artificial division, at least in this section. Welsh (1983) hypothesized that E. untermannii and E. carringtonae are most closely related to E. compactus, and they are included here on that basis.

Erigeron rhizomatus, which was included by Cronquist (1947) in sect. Wyomingia, is placed in sect. Linearifolii in the present treatment with its sister species, E. lepidopodus.

SOUTH AMERICAN GROUPS - POSITION IN ERIGERON UNKNOWN

Erigeron sect. Leptostelma (D. Don) Benth. & Hook., Gen. Pl. 2:280. 1873.

Based on Leptostelma D. Don in Sweet. TYPE: Leptostelma maximum D. Don [E. maximus (D. Don) DC.].

Additional species of sect. Leptostelma (see Solbrig 1962): E. tucumanensis Cabrera and E. tweediei Hook. & Arn.

Darwiniothamnus Harling, Acta Horti Berg. 20(3):108. 1962. TYPE: D. tenuifolius (Hook. f.) Harling (=Erigeron tenuifolius Hook. f.).

The two species of Erigeron that occur on the Galapagos Islands (E.tenuifolius and E. lancifolius Hook. f.) were segregated as the genus Darwiniothamnus by Harling (1962). These plants were said to differ from Erigeron in the following features: habit completely fruticose; involucre obconic to narrowly campanulate; phyllaries strongly imbricate in 4-6 unequal series, the outer grading into peduncular bracts; ray flowers more numerous than the disc flowers; achenes "slightly but distinctly" dimorphic, the ray achenes longer with fewer and weaker nerves than the disc achenes; and the embryo sac development monosporic.

The putatively distinctive features in Darwiniothamnus of phyllary arrangement and involucial shape can be found in many species in different sections of Erigeron. Examples of slight achenial dimorphism can be found in sect. Fruticosus, sect. Polyactis and probably others, although the usual case is for the ray achenes to have more numerous and thicker ribs than those of the disc. The reduced number of disc flowers in the Galapagos plants is unusual in continental American species of Erigeron, but a number of Caribbean species have very small heads and a correspondingly reduced number of flowers. The embryology of relatively very few species (ca 25, none from South America) of Erigeron has been investigated (Harling 1951). Two of these, however, were shown by Harling himself to have strictly monosporic embryo sac development [E. philadelphicus (sect. Olygotrichium) and E. peregrinus (sect. Fruticosus]; other species are variably mono-, bi- or tetra-sporic. In summary, the primary difference separating the two Galapagos Islands species from others of the genus is the peculiar, shrubby habit, and in my estimation this is inadequate justification for segregating them as a different genus. A case might be made, however, for regarding them as a section, but I leave this to someone more familiar with South American taxa.

The tendency for the evolutionary development of a woody habit in insular plants is well documented. Carlquist (1974) provided examples of Compositae and many other families in which genera with herbaceous mainland species have developed woody, insular species. Among those in the Compositae are insular species of Bidens, Centaurea, Dubautia, Perityle, Remya, Robinsonia, Senecio, Sonchus and Stephanodoria. As in Darwiniothamnus, most of these are rosette trees or rosette shrubs with long, mostly unbranched stems and leaves clustered near the stem tips.

Besides those of the Galapagos Islands, suffrutescent species of *Erigeron* with similar habits also have developed on the Revillagigedo Islands (noted below), the Bahama Islands (*E. darrellianus* Hemsl., tentatively placed in sect. *Olygotrichium*) and the Juan Fernandez Islands (see comments following *Terranea*). Among these, the species of the Revillagigedo Islands are most similar in habit and other characters to those of the Galapagos Islands, and in contrast to I.M. Johnston's original hypothesis of the relationship of the

latter with sect. Caenotus, I place them in Erigeron sect. Cincinnactis, which otherwise comprises species of the Mexican mainland. The habital similarity in these insular taxa almost certainly has resulted from convergent evolution.

Terranea Colla, Mem. Reale Accad. Sci. Torin. 38:11. 1835. TYPE: T. fernandezia Colla [=E. fernandezia (Colla) Harling; non E. fernandezianus Solbrig].

Erigeron fernandezia was included by Solbrig (1962) in his broad concept of sect. Erigeron. Three other closely related species of Erigeron occur in the Juan Fernandez Islands and probably evolved from a single common ancestor from the mainland, perhaps E. leptorhizon DC. (Valdebenito et al. 1985).

Astradelphus Remy, Ann. Sci. Nat. Bot. ser. 3. 12:185. 1849. (=Gusmania Remy in C. Gay, Fl. Chile 4:12. 1849; non Guzmania Ruiz & Pavon, 1802). TYPE: A. chilensis (Remy) Remy (=Gusmania chilensis Remy; =Erigeron remyanus Wedd., Chlor. And. 1:195. 1857).

According to Solbrig, Erigeron remyanus is perhaps a member of sect. Erigeron (sensu Solbrig 1962).

GROUPS TRANSFERRED FROM ERIGERON TO OTHER GENERA

1. CONYZA

Erigeron sect. Caenotus Nutt., Gen. Plant. 2:148. 1818. TYPE: E. canadensis L. [=Conyza canadensis (L.) Cronq.]. Caenotus (Nutt.) Rafin., Fl. Tell. 2:50. 1836. Conyza sect. Caenotus (Nutt.) Cronq. ex Cuatr., Webbia 24:211. 1969.

Erigeron sect. Multiflori G. Don in Loudon, Hort. Brit. 343. 1830. LECTO-TYPE (designated here): E. canadensis L. [=Conyza canadensis (L.) Cronq.]. Don also included 22 other species of a number of disparate lineages.

I regard sect. Caenotus as a synonym of sect. Conyza, which includes C. canadensis (L.) Cronq., C. bonariensis (L.) Cronq., C. ramosissima Cronq., C. primulaefolia (Lam.) Lourteig & Cuatr. [=C. chilensis Spreng.] and others. See Nesom (in press) for further comments and synonymy.

2. CELMISIA

Pappochroma Rafin., Fl. Tellur. 2:48. 1836. TYPE: P. uniflora Rafin. (=Erigeron pappochroma Labill., an Australian species, perhaps Celmisia Cass., 1825).

3. ORITROPHIUM

Erigeron sect. Oritrophium (Kunth) Benth. & Hook., Gen. Pl. 2:280. 1873. Based on Aster sect. Oritrophium Kunth. LECTOTYPE (Cuatrecasas 1961): Aster pellitus Kunth [=Oritrophium peruvianum (Lam.)

Cuatr.l. Celmisia sect. Oritrophium (Kunth) Solbrig. Oritrophium (Kunth) Cuatr.

4. TRIMORPHA

PHYTOLOGIA

Erigeron sect. Trimorpha (Cass. in F. Cuvier) DC., Prodr. 5:290. 1836. Trimorpha Cass., Bull. Sci. Soc. Philom. Paris 1817:137. 1817. TYPE: Trimorpha vulgaris Cass. in Cuvier, Dict. Sci. Nat. 55:324. 1828 (=E. acris L.). Trimorphaea Cass. in Cuvier, Dict. Sci. Nat. 37:462. 1825. Erigeron subg. Trimorpha (Cass.) M. Pop.

Erigeron (sp.-group) Acres Rydb., Fl. Colorado 359. 1906, in clave. TYPE: E. acris L.

I regard Trimorpha as a distinct genus more similar to Conyza than Erigeron (Nesom 1989b).

5. GENUS UNKNOWN

Erigeron sect. Submultiflori G. Don in Loudon, Hort. Brit. 343. 1830. LECTOTYPE (designated here): E. carolinianus L. Don also included Erigeron villarsii Bell. (=Erigeron atticus Villars of sect. Trimorpha in his sect. Submultiflori.

Fernald (1944) discussed the identity of Erigeron carolinianus L. but could only conclude that he could not identify it "unless it was something not originally from Carolina or, as Dillenius thought, an abnormal individual." It is certainly not an Erigeron, and I agree with Fernald that it is unlike any species of Euthamia. It is more Solidago-like, but it is likely that the identity of this Linnaean epithet will remain equivocal. Because Don's sect. Submultiflori was essentially meaningless in comprising two extremely divergent species from different genera, I feel justified in attaching it to a species name that itself has little chance of being clearly identified. To choose E. villarsii as the lectotype would necessitate replacing the widely used and well established name of sect. Trimorpha.

Tanaxion Rafin., Fl. Tellur. 2:51. 1836. TYPE: T. tomentosum Rafin. (=Erigeron bahamensis Scop.). I do not know the identity of this plant.

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LITERATURE CITED

- Ake, K.M. 1984. Systematics of six species of Erigeron L. section Erigeron (Asteraceae). M.S. Thesis, University of Montana, Missoula.
- Atwood, N.D. & S.L. Welsh. 1988. An *Erigeron* from Nevada and a *Penstemon* from Idaho. Great Basin Naturalist 48:495-498.
- Becker, K.M. 1976. A new species of Erigeron (Asteraceae) from Alaska and Yukon. Brittonia 28:144-146.
- Bentham, G. & J.D. Hooker. 1873. Genera Plantarum, Vol. 2(1). L. Reeve & Co., London.
- Botschantzev, V.P. 1959. Erigeron. Pp. 191-288 in Flora U.R.S.S., vol. 25, ed. V.L. Komarov. U.S.S.R. Acad. Sciences, Leningrad.
- Brunsfeld, S.J. & G.L. Nesom. (in press). Erigeron salmonensis (Asteraceae), a rare new species from Idaho. Brittonia 41:.
- Carlquist, S. 1974. Island Biology. Columbia Univ. Press, New York.
- Cronquist, A. 1947. Revision of the North American species of Erigeron, north of Mexico. Brittonia 6:121-302.
- Fernald, M.L. 1944. Is Erigeron carolinianus a valid American species? Rhodora 46:323-330.
- Gray, A. 1884. Synoptical Flora of North America. Vol. 1, part 2. Ivison, Blakeman, Taylor & Co. New York.
- Grierson, A.J.C. & K. H. Reichinger. 1982. Compositae V Astereae. Flora Iranica 154:1-70 (+76 figures).
- Harling, G. 1951. Embryological studies in the Compositae:III. Astereae. Acta Horti Berg. 16:73-120.
- _____. 1962. On some Compositae endemic to the Galapagos Islands. Acta Horti Berg. 20:63-120.
- Holmgren, N.H. 1979. Subgeneric and sectional names for Intermountain *Penstemon* (Scrophulariaceae). Brittonia 31:358-364.
- Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, California.
- Jones, A.G. 1980. A classification of the New World species of Aster (Asteraceae). Syst. Bot. 32:230-239.
- Loudon, J.C. 1830. Loudon's Hortus Britannicus Printed for Longman et al., London.
- Macbride, J.F. & E.B. Payson. 1917. A revision of the Erigerons of the series *Multifidi*. Contr. Gray Herb. 49:72-79.

- Maguire, B. 1944. Great Basin plants—VIII. New species in *Carex* and *Erigeron*. Brittonia 5:199-202.
- Nesom, G.L. 1976. A new species of Erigeron (Asteraceae) and its relatives in southwestern Utah. Brittonia 28:263-272.
- _____. 1982. Systematics of the Erigeron rusbyi group (Asteraceae) and delimitation of sect. Peregrinus. Syst. Bot. 7:457-470.
- Astereae). Phytologia 66:415-455.
- _____. 1989b. The separation of Trimorpha (Compositae: Astereae) from Erigeron. Phytologia 67:61-66.
- _____. (in press). Further definition of the genus Conyza (Compositae: Astereae). Phytologia 67:.
- _____ & V.D. Roth. 1981. Erigeron scopulinus (Compositae) an endemic from the southwestern United States. J. Arizona Nevada Acad. Sci. 16:39-42.
- & S. Sundberg. 1985. New combinations in Erigeron (Asteraceae). Sida 11:249-250.
- ______, L. A. Vorobik & R. L. Hartman. (submitted). Recent collections, identity, and classification of Aster blepharophyllus (Asteraceae: Astereae). Syst. Bot.
- Nuttall, T. 1818. Genera of North American plants. Reprint by Hafner Publ. Co., New York, 1971.
- ______. 1840-41. Descriptions of new species and genera of plants in the natural order of the Compositae, etc. Trans. Amer. Philos. Soc. ser. 2, 7:283-453.
- Rafinesque, C.S. 1836. Flora Telluriana. Philadephia: H. Probasco. (Facsimile reprint, Arnold Arboretum, 1946).
- Rydberg, P.A. 1906. Erigeron. In: Flora of Colorado. Agric. Exp. Sta. Agric. Coll. Colorado Bull. 100:359-366.
- ______. 1918. Erigeron. In: Flora of the Rocky Mountains and Adjacent Plains. Pp. 896-911. Hafner Publishing Co., New York.
- Solbrig, O.T. 1960. The South American sections of Erigeron and their relation to Celmisia. Contr. Gray Herb. 188:65-86.
- Herb. 1962. The South American species of Erigeron. Contr. Gray
- Spongberg, S.A. 1971. A systematic and evolutionary study of North American arctic and alpine monocephalous species of *Erigeron* (Compositae). Ph.D. dissertation, University of North Carolina, Chapel Hill.

- Strother, J.L. & W. J. Ferlatte. 1988. Review of *Erigeron eatonii* and allied taxa (Compositae: Astereae). Madroño 35:77-91.
- Sundberg, S.D. 1986. The systematics of Aster subg. Oxytripolium (Compositae) and historically allied species. Ph.D. dissertation, University of Texas, Austin.
- & A.G. Jones. 1987. Loudon's Hortus Britannicus (1830): An early source of sectional names, necessitating nomenclatural changes in many genera—Aster: A case in point. Taxon 36:97-98.
- . 1988. Loudon's Hortus Britannicus: A correction. Taxon 37:151.
- Torrey, J. & A. Gray. 1841. A Flora of North America, vol. 2, part 1. New York: Wiley & Putnam.
- Valdebenito, H., T.F. Stuessy & D.F. Crawford. 1985. Evolution of the genus *Erigeron* in the Juan Fernandez Islands, Chile. Amer. J. Bot. (Abstracts) 72:974. 1985.
- Vierhapper, F. 1906. Monographie der alpinen Erigeron—Arten Europas und Vorderasiens. Beih. Bot. Centralbl. 19:385-560.
- Welsh, S.L. 1983. A bouquet of daisies (Erigeron, Compositae). Great Basin Naturalist 43:365-368.
- Basin Naturalist 46:261-264.

DOS NUEVOS REGISTROS DE ARISTOLOCHIA (ARISTOLOCHIACEAE) PARA VERACRUZ, MÉXICO

José Ortega Ortíz Universidad Veracruzana, Xalapa, Veracruz, MÉXICO

RESUMEN

Aristolochia arborea Linden y A. pilosa H.B.K. se registran por primera vez para el estado de Veracruz, la primera de la región de Uxpanapa y la segunda cerca de Las Choapas. Se discuten las distribuciones, habitats, afinidades y relaciones de estos taxa.

PALABRAS CLAVES: Aristolochiaceae, Aristolochia arborea, A. pilosa, Uxpanapa, Las Choapas, Veracruz.

ABSTRACT

Aristolochia arborea Linden and A. pilosa H.B.K. are recorded for the first time for the state of Veracruz, the former in the Río Uxpanapa watershed, and the latter near Las Choapas. Their known distributions, habitats and relationships are discussed.

KEY WORDS: Aristolochiaceae, Aristolochia arborea, A. pilosa, Uxpanapa, Las Choapas, Veracruz.

Durante el estudio taxonómico de la familia Aristolochiaceae que el autor realizó para la Flora de Veracruz (Ortega Ortíz 1988), se encontraron ejemplares de Aristolochia arborea y A. pilosa, los cuales constituyen nuevos registros para el estado.

Aristolochia arborea (Figure 1) se describió tomando como base los especimenes colectados por Ghiesbreght en el estado de Chiapas, de localidad desconocida. Esta especie se encuentra distribuída en las selvas altas perennifolias del sureste de México (Chiapas, Tabasco, Veracruz y probablamente Oaxaca), Guatemala y El Salvador. Pfeifer (1966) incluyó a A. steyermarkii Standl. como sinónimo de A. arborea, aunque posteriormente Barringer (1983) encontró diferencias que justifican su reconocimiento como una especie distinta. Aristolochia steyermarkii es un arbusto con flores axilares, y el limbo de la flor tiene una protuberancia sésil y rugosa (la ampolla),

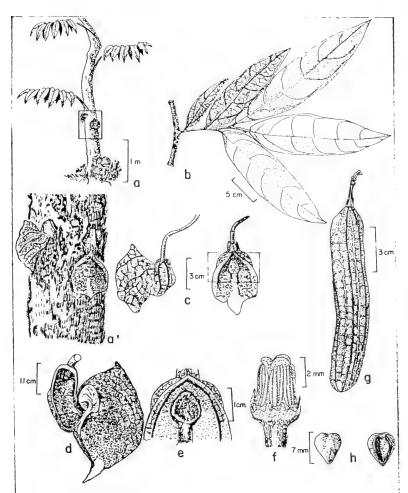


Fig. 1. Aristolochia arborea. a, Forma biológica; a, recuadro del tallo, mostrando las flores caulinares; b, rama con hojas; c, flor (en vista lateral y frontal); d, corte transversal de la flor mostrando el ginostemo y la ampolla; e, recuadro de la flor, mostrando en detalle la ampolla; f, ginostemo; g, fruto; h, semilla. Ilustración por Seatiel Guiochin, basada en fotografías de Dorantes et al. 2957 (a, a') y en ejemplares de J. Ortega y R. Ortega 348 (b, c, d, e, f, g, h).

a diferencia de A. arborea que presenta flores caulinares y el limbo posee una ampolla estipitada. Las especies anteriores están estrechamente relacionadas con A. impudica Ortega (Ortega, 1987), la cual se distingue por la presencia de una inflorescencia de 32-50 cm de largo, los pedicelos geniculados de 6-13 cm de largo, una ampolla de 2.5-4 cm de largo, 2-5 cm de ancho, y el margen revoluto de los lóbulos laterales del limbo del cáliz.

Aristolochia arborea ha sido escasamente colectada. Posee una distribución que corresponde, en parte, a un área de alta precipitación que se extiende desde el S de Veracruz y S de Tabasco al N de Chiapas, pero que no se continua hasta Guatemala. Esta zona corresponde a un refugio de elementos tropicales durante el Pleisticeno tardío (Wendt 1985). Sin embargo, esta especie continua su distribución hasta Guatemala y El Salvador (Figure 2).

Aristolochia pilosa es una liana de amplia distribución desde México hasta el norte de Sudamérica. Recientemente ha sido encontrada cerca de Las Choapas, Veracruz, entre Nanchital y Cuichapa en altitudes ca de 50 m. Ocurre principalmente cerca de arroyos o a la orilla de carreteras sobre pequeños arbustos, en suelos arenosos con vegetación secundaria de selva baja caducifolia. Aristolochia pilosa se reconoce facilmente por el indumento abundante y ferrugíneo que se presenta en toda la superficie externa de la planta, así como su flor, cuyo limbo es espatulado-oblongo con papilas moreno oscuras en el apice, y por el fruto de 5-7.5 cm de largo.

A continuación se presenta una descripción breve de A. arborea y A. pilosa basada en los ejemplares de Veracruz.

Aristolochia arborea Linden, Cat. Pl. Exot. 13:6. 1858. TIPO: MÉXICO: Chiapas, Ghiesbreght s.n. (Holotipo BM).

Arbustos pequeños, perennes, de 3-5 m de alto; tallo erecto. Hojas alternas, aromaticas, lanceoladas, 8-26 cm de largo, 2-6.5 cm de ancho; ápice acuminado o caudilado, base redondeada y obtusa. Inflorescencia cauliflora, racemosa, 5-8 cm de ancho; flores bisexuales, cáliz geniculado, de color púrpura-guinda, utrículo ovoide-elipsoide, siringe ausente, tubo doblado, limbo trilobado, lóbulo central mas largo, con una mancha blanca en el ápice, una ambolla purpurea, globosa-capitada, esponjosa y con pelos glandulares por arriba del orificio del tubo, de 1 cm de largo y un estípite de 8-9 mm de largo; estambres 6, en un ginostemo con 3 lóbulos estigmáticos y 2 anteras por lóbulo. Fruto una cápsula cilindrica, ligeramente doblada, 10-13 cm de largo, 2.5-3.5 cm de ancho; semillas cordiforme-triangulares, 5-7 mm de largo y ancho.

Ejemplares examinados. MÉXICO: Veracruz. Mun. Hidalgotitlán, km 0-2 al S del campamento Hnos. Cedillo, camino a Río Alegre, desviación al E, 140 m, 23 May 1974, *Dorantes et al. 2957* (ENCB, MEXU, XAL); km 3 del campamento Hnos. Cedillo-Río Alegre, 150 m, 30 Ago 1974, *Dorantes et al. 3557* (XAL).

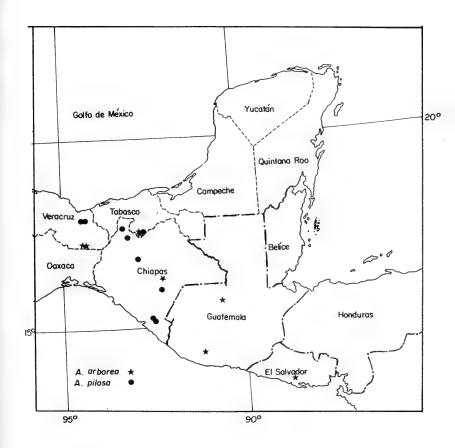


Fig. 2. Mapa de la distribución de Aristolochia arborea Linden y A. pilosa H.B. & K., basado en ejemplares examinados en este trabajo.

PHYTOLOGIA

Nombre Local. Flor de Chapo, Pachuli (Tabasco), Tecolotillo (Guatemala). Usos. El tallo se utiliza como febrífugo.

Ecología: Selva alta perennifolia, cerca de ríos, arroyos y lugares montanosos, sobre suelos calcáreos y pedregosos.

Aristolochia pilosa H.B.K., Nov. Gen. Sp. 2:156. 1819. TIPO: ECUADOR: ca Guayaquil, Humboldt & Bonpland s.n. (Holotipo B; foto XAL!).

Liana, perenne, 2-5 m de largo, el tallo piloso o hirsuto. Hojas cordiformes, 9-14.5 cm de largo, 7-10 cm de ancho, membranaceas, la haz glabrascente, el envés densamente piloso o hirsuto, el margen entero, el ápice redondo u obtuso, la base cordada; pecíolo cilindrico, 3-4 cm de largo, piloso o hirsuto. Inflorenscia axilar, solitaria, 6-14.5 cm de largo, 1-2 cm de ancho; flores bisexuales, de color verde amarilento y púrpura; cáliz arcuado, 6-8.5 cm de largo, 1-2 cm de ancho, piloso-hirsuto en la superficie externa, el utrículo verde amarillo, ovoide o subpiriforme, 1.8-2.5 cm de largo, 1-1.5 cm de ancho, lanuloso-flocoso en la parte interna, el siringe de color crema, un ligero borde inequilátero en el interior, ca 1 mm de largo, 5-7 mm de ancho, opaco y glabro, el tubo verde amarillo, rectilíneo-arcuado, 1.8-2.5 cm de largo, 0.3-0.5 cm de ancho, opaco, con pelos estrigosos en la superficie interna; el limbo con un solo lóbulo, de color púpura y amarillo, espatulado-oblongo, 3-5.5 cm de largo, 1-2 cm de ancho, brillante, esparcidamente fimbriado en la superficie interna, el margen involuto, la base redondo-cordada; estambres 6, insertos en un ginostemo capitado, 5-8 mm de largo, 3-6 mm de ancho, anteras 1 por lóbulo. Fruto capsular, leñoso, elipsoide, 5-7.5 cm de largo, 1.5-2 cm de ancho, septifraga, piloso-hirsuto; semillas de color moreno claro-moreno oscuro, planas, triangular-cordiformes, 4-5 mm de largo, 3-4 mm de ancho y 0.5-0.7 mm de grueso, el margen entero, el ápice agudo, la base cordada, la testa delgada y aceitosa, granulosa, pubérula; endospermo abundante.

Ejemplares examinados: MÉXICO: Veracruz. Mun. Coatzacoalcos, 10 km WNW of Las Choapas on road to Nanchital, 50 m, 2 Ene 1986, Nee 32464 (NY, XAL); Carretera Nanchital-Las Choapas, 2 km antes de llegar a la desviación a Chuichapa, 20 Jun 1987 Ortega, McDonald & Aguilar 507 (XAL).

Nombre local: Huehuecho, huehueche, pecho de paloma, curanina (Chiapas); sombrerito, hediondilla (Guatemala).

Ecología: Selva baja caducifolia, vegetación secundaria de selva alta perennifolia, ruderal.

Floración, Julio a Enero.

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REFERENCIAS

- Barringer, K. 1983. Aristolochiaceae. En: Flora Costaricensis. Field Mus. Nat. Hist., Bot. 13:79-87.
- Ortega Ortíz, J. 1987. Notas del herbario XAL. IX. Dos especies nuevas hexandreas de *Aristolochia* (Aristolochiaceae) de Veracruz, México. Biótica 12:209-216.
- _____ 1988. Aristolochiaceae. En: Flora de Veracruz (en comité editorial).
- Pfeifer, H.W. 1966. Revision of the North and Central American hexandrous species of *Aristolochia* (Aristolochiaceae). Ann. Missouri Bot. Gard. 53:115-196.
- Wendt, T. 1985. A new simple-leaved species of *Recchia* (Simaroubaceae) from Southeastern Mexico. Brittonia 37:219-225.

CONTRIBUTION TO THE LICHEN FLORA OF VENEZUELA, VII

Manuel López-Figueiras y Antonio Morales Méndez Instituto de Investigaciones, Facultad de Farmacia, Universidad de Los Andes, Mérida, VENEZUELA

ABSTRACT

Several new distribution records for *Pyxine* are reported from Venezuela.

KEY WORDS: Floristics, lichens, Pyxine, Venezuela, Neotropics.

Study of *Pyzine* in Venezuela has been superficial, mainly due to the small number of collectors and the lack of correctly identified herbarium specimens.

Vareschi (1973) and López-Figueiras (1986), respectively mentioned seven and five species present in Venezuela.

Later relationships of one of us (A.M.M.) with Dr. K. Kalb [monographer of the Brasilian pyxines (1987)], has allowed an increase in accurate herbarium specimens by his kindly help in botanical identification of our material.

The results of these studies are reported as follows:

Pyzine berteroana (Fée) Imsh.

Estado Falcón: Alrededores de Sinamaica, proximidades de Cerro Azul (Sierra Ziruma o Empalado), López-F. 21571.

Estado Mérida: Mocomboco, Aricagua, López-F. 8969,12607.

Pyxine caesiopruinosa (Nyl.) Imsh.

Estado Lara: En Pico-Pico (Sierra de Bobare), López-F. & R. Smith 20768-B.

Estado Mérida: El Pedregal de Jalí, junto a La Carbonera, López-F. 18145, 18174.

Estado Táchira: Proximidades de Providencia, cercanías de Rubio, carretera (vieja) San Cristóbal-Rubio, López-F. 25613.

Estado Trujillo: Las Palmas, carretera Carache-Agua de Obispo, López-F. 28020; Cercanías de Santa Ana de Trujillo, carretera Boconó-Valera, López-F. 28130; Vertiente oriental del páramo del Guache, Los Cortijos, cercanías de Carache, López-F. 28398,28411.

Pyxine cocoes (Sw.) Nyl.

Estado Falcón: Paraguaná: ví Coro-Adícora, López-F. 19190; entre El Hato y Pueblo Nuevo, López-F. 19217; el Balsamal, vía Pueblo Nuevo hacia el Vínculo, López-F. 21242,21244; a lo largo de Monte Cano, López-F. 21262; Cerro Santa Ana, a lo largo del arroyo Santa Ana, López-F. 21345; a lo largo del arroyo Siraba, López-F. 21349; NW del cerro Santa Ana frente a Bella Vista, López-F. 21743; Punta Prudencio, al suroeste de Tacuato, López-F., R. Wingfield & A. Morales 32495. Inmediaciones del río Ricoa, vía Coro-Morón, López-F. 21691. Entre La Cruz y La Goya, ví Coro-Churuguara, López-F. 21878. Sierra San Luis, alrededores de la Piedra Campana, entre Carrizalito y Cucaire, López-F. & R. Wingfield 22405,22406. Proximidades del río Japure, entre Paso Calderas y Buruica, vía Pedregal-Tapure, López-F. & R. Wingfield 22510.

Estado Lara: Sierra Portuguesa, Loma El León, cercanías de Barquisimeto,

López-F. & R. Smith 21168.

Estado Mérida: Arriba de Las González, carretera Mérida-Lagunillas, López-F. 16294; zona xerófila de Lagunillas, López-F. 18031.

Estado Trujillo: Entre Carache y La Cuchilla, López-F. 22278.

Pyxine cognata Stirt.

Estado Mérida: Alrededores de Minzal, cercanías de Mesa Quintero, vía hacia Pico de Horma, López-F. 23238; La Sabana, área de Pico de Horma, al suroeste de Mesa Quintero, López-F. & H. Rodríguez 23331; Parque Nacional Sierra Nevada, alrededores de La Mucuy, López-F. & H. Rodríguez 27184,27236.

Estado Táchira: Márgenes del río Pedernales, Laguna Garciá, zona de Pregoneros, López-F. & A. Morales 32461.

Estado Trujillo: Páramo de Cendé, López-F. 12992.

Pyxine coralligera Malme

Estado Lara: Parque Nacional Yacambú, Sierra Portuguesa, López-F. 15729,15976.

Estado Mérida: Finca Los Topes, entre Chiguará y La Trampa, López-F. & A. Morales 31005.

Estado Táchira: Márgenes del río Pedernales, Laguna Garciá, cercanías de Pregoneros, López-F. & A. Morales 32454-A.

Estado Trujillo: Entre El Filo de San Isidro y La Becerrera, a 25 km de La Concepción de Carache, por la carretera nueva, López-F. & H. Rodríguez 28063.

Pyxine daedalea Krog & R. Sant.

Estado Mérida: Mocomboco, Aricagua, López-F. 12602; San Juanito, Chiguará, A. Morales 116.

Pyxine endolutea Kalb

Estado Mérida: El Maciegal, cuenca del río La Pedregosa, cercanías de Mérida, López-F. 10643; Finca Los Topes, cercanías de Chiguará, López-F. & A. Morales 32473.

Estado Trujillo: Carretera (vieja) Trujillo-La Cristalina-Boconó, López-F. & M. Keogh 11240,11248,11249,11257; Los Cortijos, vertiente oriental del páramo del Guache, cercanías de Carache, López-F. 28388.

Pyxine eschweileri (Tuck.) Vain.

Estado Lara: Sabanas El Altar-Yaritagua, proximidades de un puente sobre el río Turbio, López-F. & R. Smith 16479.

Estado Mérida: Sierra Nevada de Mérida, quebrada Fafoy, cercanínas de El Carrizal, López-F. & M. Hale 20123, 20174, 20274.

Pyxine limbulata Müll. Arg.

Estado Mérida: Páramo de Piñago, vía Piñago, a lo largo de la carretera entre las quebradas Las Tapias y Piñago, López-F. 27745.

Esta especie es primera cita para el hemisferio occidental.

Pyxine microspora Vain.

Estado Lara: Sierra Portuguesa, Loma El León, proximidades de Barquisimeto, López-F. & R. Smith 21148.

Estado Mérida: El Pedregal de Jalí, junto a La Carbonera, López-F. 18171.

Pyxine petricola Nyl. in Cromb.

Estado Lara: Hacienda Los Cristales, vía Barquisimeto-Sarare, López-F. 16089; El Gamelotal, vía Barquisimeto-El Altar-Yaritagua, López-F. 16130-B; entre Barbacoas y San Pedro, López-F. 19025,19039,19064,19067,19072, 20813; Sierra Portuguesa, Loma El León, proximidades de Barquisimeto, López-F. & R. Smith 21180,21210; Sierra Ziruma o Empalado, en el Carrón, López-F. & R. Smith 20813.

Estado Mérida: Arriba de Las González, carretera Mérida-Lagunillas, López-F. 16292,16299-B,16300-B,16303-A,16303-B; Zona xerófile de Lagunillas, López-F. 18053,18055-A; El Pedregal de Jalí, junto a La Carbonera, López-F. 18156; Arriba de Tovar en la carretera hacia el Páramo de Mariño, López-F. 24695; Proximidades de Mesa Bolívar, cercanías del entronque de la carretera Mesa Bolívar-El Vigía, López-F. 25540-B.

Estado Táchira: Las Coloradas, zona xerófila de La Grita, López-F. 14409; alrededores de Salomóm, vía San Cristóbal-Cordero-Alto de El Zumbador, López-F. 24803.

Estado Trujillo: Páramo de La Naríz, alrededores de T.V., López-F. 16680-A; entre Carache y La Cuchilla, López-F. 22271; En Florencia, páramo El Turmal, inmediaciones del camino hacia el páramo Cendé, López-F. 30734.

Pyxine pungens Zahlbr.

Estado Lara: Sierra de Barbacoas entre San Pedro y Barbacoas, $L\acute{o}pez ext{-}F.$ 18983-B.

Estado Mérida: Mocomboco, Aricagua, López-F. 12610; El Pedregal de Jalí, junto a La Carbonera, López-F. 18169,26795; La Carbonera, cercanías de Mérida, López-F. 22058; El Valle cercanías de Mérida, López-F. 29295.

Pyxine pyxinoides (Müll. Arg.) Kalb

Estado Mérida: El Paramito, un sector de La Carbonera, López-F. 17523.

Pyxine rhodesica Vain ex Lynge.

Estado Mérida: Mocomboco, Aricagua, López-F. 12608; Finca San Isidro, La Carbonera, vía La Azulita, López-F. 26748; La Carbonera, López-F. 30086.

Pyxine subcinerea Stirt.

Estado Falcón: Sierra de San Luis, La Chapa, vía Las Negritas-Uria, López-F. 19241.

Estado Lara: A lo largo de la carretera entre Guárico y Chubasquín, López-F. 17207-B,17208.

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LITERATURE CITED

- Kalb, K. 1987. Brasilianishe Flechten. 1. Die Gattung Pyzine. Bibl. Lichenol., J. Cramer, Berlin-Stuttgart.
- López F., M. 1986. Censo de Macrolíquenes Venezolanos de los Estados Falcón, Lara, Mérida, Táchira y Trujillo. U.L.A., Facultad Farmacia 1-521.
- Vareschi, W. 1973. Catálogo de Líquenes de Venezuela. Acta Bot. Venez. 8(1-4):177-245.

NEW COMBINATIONS IN ERICAMERIA (COMPOSITAE: ASTEREAE)

Guy L. Nesom Department of Botany, University of Texas, Austin, Texas 78713 USA

ABSTRACT

Two new combinations in *Ericameria* are proposed: E. palmeri var. pachylepis and E. parishii var. peninsularis.

KEY WORDS: Ericameria, Haplopappus, Asteraceae, México, systematics.

In the preparation of a taxonomic treatment of the Mexican species of *Ericameria*, two new combinations are necessary.

Ericameria palmeri (A. Gray) H.M. Hall var. pachylepis (H.M. Hall) Nesom, comb. nov. Based on *Haplopappus palmeri* subsp. pachylepis H.M. Hall, Carnegie Inst. Washington Publ. No. 389:267. 1928. *Haplopappus palmeri* var. pachylepis (H.M. Hall) Munz, Man S. Calif. 522. 1935.

Ericameria palmeri is recognized by its strictly erect stems and ovate-cylindric capitulescences with radiate heads. Var. pachylepis, the northern variant of the species, which ranges from Riverside County, California, northward to Ventura County, differs from var. palmeri primarily in its larger leaves (5-16 mm vs 10-40 mm long) and the broader, more definite gland on the apical half of the phyllaries. Differences noted by Munz (1974) in the involucre height and number of ray and disc flowers separate the two taxa inconsistently.

Ericameria parishii (E. Greene) H.M. Hall var. peninsularis (R. Moran) Nesom, comb. nov. Based on *Haplopappus arborescens* subsp. peninsularis R. Moran, Trans. San Diego Soc. Nat. Hist. 15:152. 1969.

The three taxa of the Ericameria arborescens (A. Gray) H.M. Hall group occupy three separate geographic zones. Moran (1969) recognized each of the three as a subspecies of E. arborescens (subsp. arborescens, subsp. parishii (E. Greene) R. Moran and subsp. peninsularis R. Moran), but all other studies of the California flora have maintained E. arborescens and E. parishii as distinct species. Ericameria arborescens, the northernmost form, apparently does not

intergrade morphologically with E. parishii, which is restricted to southern California, where their ranges meet in southern California.

On the other hand, Ericameria parishii var. parishii and var. peninsularis, which is endemic to Baja California Norte, are similar in all respects except leaf shape, and according to Moran (1969), they intergrade in this character. "Since some specimens are virtually identical, [var. peninsularis] can scarcely be treated as a species separate from [E.] parishii" (Moran 1969, p. 154). Hall's concept of E. parishii (1928) also included var. peninsularis, because he cited as E. parishii a collection from Sierra San Pedro Martir (Robertson 48, UC) that was included by Moran as var. peninsularis. Moran's solution in identifying all three taxa as subspecies of one species emphasized their close relationship but disregarded the clear discontinuity between E. arborescens and E. parishii as well as the greater similarity between var. parishii and var. peninsularis. In my view, these taxa are best identified by the following synoptic key.

- 1. Heads on ultimate peduncles 0-5 mm long, in compact cymes; disc flowers 8-18 per head, glabrate to very sparsely papillate or minutely hairy on the tube(2)
 - 2. Leaves linear-oblanceolate to linear, 1.5-2.0 (-3.5) mm wide E. parishii var. peninsularis
 - 2. Leaves narrowly elliptic to elliptic-oblanceolate, 3-10 mm wide E. parishii var. parishii

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LITERATURE CITED

Hall, H.M. 1928. Sect. Ericameria, in The Genus Haplopappus—A phylogenetic study in the Compositae. Carnegie Inst. Washington, Publ. 389:258-288.

- Munz, P.A. 1974. Haplopappus. Pp. 174-181 in Flora of Southern California. Univ. California Press, Berkeley.
- Moran, R. 1969. Five new taxa of *Haplopappus* (Compositae) from Baja California, Mexico. Trans. San Diego Soc. Nat. Hist. 15:149-164.
- Urbatsch, L.E. & J.R. Wussow. 1979. The taxonomic affinities of *Haplopappus linearifolius* (Asteraceae Astereae). Brittonia 31:265-275.

A NEW SPECIES OF VERBESINA SECTION VERBESINARIA FROM THE DOMINICAN REPUBLIC

John Olsen Department of Biology, Rhodes College, Memphis, Tennessee 38112 USA

ABSTRACT

Verbesina howardiana is described from Hispañola.

KEY WORDS: Asteraceae, Verbesina, Lesser Antilles, systematics.

During the preparation of the Flora of the Lesser Antilles, the following new taxon was revealed.

Verbesina howardiana Olsen, sp. nov. TYPE: DOMINICAN REPUB-LIC: St. Paul Parish. Morne Trois Piton, 4400 ft, barren area on mountain top, 23 Oct 1964, D.H. Nicolson 1815. (holotype: GH).

Frutex ca 1 m altus; cauli exalati, valde cicatricibus foliorum notati. Folia fasciculata sub capitulis, laminae obovatae, apex acute latus ad rotundatem, folia margine minutissime serrata; supra glabrescentia, subtus resinose pubescentia dense in nervis. Capitula ca 1.5 cm diametro; flores radii 19-21, ligulae luteae, ca 11-15 mm longae; flores disci numerosi corollae luteae, tubi glabri. Achaenia nigra, glabra, alae non latae; pappus biaristatus, inaequalis.

Shrub to 1.0 m tall; stems terete, pithy, unwinged, nearly glabrous below and strongly marked by prominent leaf scars, becoming densely pubescent above. Leaves clustered below the capitulescence, obovate, to 12.0 cm long, 7.0 cm wide, apex rounded to broadly acute, base narrows to a short resinous pubescent petiole, ≤ 1.0 cm long, margins revolute, minutely serrate, blade glabrous above or with a few resinous hairs along the midvein, densely resinous pubescent along all veins below, very sparsely pubescent on the blade surface. Capitulescence a loose corymb of 12-20 heads on densely pubescent peduncles to 6.0 cm long; heads to 1.5 cm in diameter, excluding the rays. Involucre 2-3 seriate, outer series oblong, 3.0-4.5 mm long, 1.2-1.5 mm wide, inner series oblanceolate, 5.0-5.8 mm long, 1.2-1.5 mm wide, apex rounded to broadly acute, pubescent at the base only, margins not ciliate. Pales 6.5-8.0

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mm long, 1.7-2.0 mm wide, glabrous, apex herbaceous, margins not ciliate. Rays 19-21, yellow, ligules 11-15 mm long, 3.2-3.5 mm wide, apex minutely 3dentate, styles well exserted from the tube; tube 1.8-2.0 mm long, 0.4-0.5 mm wide, pubescent. Disc florets numerous, ca 75, corolla yellow, tubular, 3.8-4.0 mm long, 1.4-1.5 mm wide, tube 1.5 mm long, 0.5 mm wide, glabrous. Ray achenes black, glabrous, 5.0-5.5 mm long, 1.3-1.5 mm wide, thinly winged, wings < 0.2 mm wide; awns unequal, to 4.5 mm long. Disc achenes black, glabrous, 5.3-5.5 mm long, 1.7-2.0 mm wide, thinly winged, wings < 0.3 mm wide; awns unequal, to 5.0 mm long.

Additional specimens examined (all come from Morne Trois Piton): K.L. Chambers 2588 (GH); W.H. Hodge 1397 (GH); C. Kimber 975 (GH [2 sheets]).

V. howardiana is a member of section Verbesinaria. All collections of this taxon have been from elevations above 4000 ft, at or near the summit of Morne Trois Pitons in areas described as rain forest (400 inches per year) where it grows in open areas.

V. howardiana is related to several Caribbean taxa including V. guadeloupensis Urb., V. karsticola Proctor and V. caymanensis Proctor, V. howardiana is easily differentiated from V. quadeloupensis on the basis of its corky stem with prominent leaf scars and obovate leaves. It also has a completely glabrous tube on the disc floret. The Urban species has lanceolate leaves, lacks the prominent leaf scars and has a pubescent tube on the disc florets. Both V. caymanensis and V. karsticola are members of section Ochractinia. V. caymanensis has the prominent leaf scars seen in V. howardiana, but has white florets and the leaves are serrate to weakly lobed, especially at the apex. V. karsticola has a leaf morphology which more closely matches V. howardiana, but again has white florets and lacks the prominent leaf scars.

It is a pleasure to name this taxon for Dr. Richard Howard who brought it to my attention during his preparation of the Flora of the Lesser Antilles.

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